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SOLENOPOTES CAPILLATUS, A SUCKING LOUSE OF CATTLE NOT HERETOFORE KNOWN IN THE UNITED STATES

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INTRODUCTION

In 1904 Enderlein[1] described a single male sucking louse taken on cattle in Leipsic, Germany, as a new genus and species, *Solenopotes capillatus*. Apparently no further reference was made to this insect until 1916, when Ferris[2] incidentally mentioned the species, stating that he considered the Enderlein type specimen as being immature and concluding that the species was a synonym of *Linognathus vituli* L.

In examining the specimens of Anoplura in the collection of the Dallas laboratory of the Bureau of Entomology in 1917, H. P. Wood noted that some of the material collected on cattle did not appear to be either *Linognathus vituli* L. or *Haematopinus eurysternus* Nitzsche. This led to a search of literature for other species recorded from this host, and the references mentioned above were found. Upon comparing the material in question with Enderlein's description it was evident that it was *Solenopotes capillatus*.

Material in the collection at the Dallas laboratory indicates that the species has a wide distribution in the United States, and notes upon it show that at times it may become a serious cattle pest. Data on the collections are as follows:

Bishopp No. 9192, Dallas, Tex., March 20, 1910, many specimens on bull (*Bos taurus* L.) in laboratory yard, F. C. Bishopp, collector; Bishopp No. 2681, Viewpoint, Oreg., March 8, 1913, heavy infestation of range cattle (*B. taurus*), H. H. Hatch, collector; No. 4292, Riverside, Md., February 14, 1915, on calves, F. C. Bishopp, collector; No. 7485, Dallas, Tex., November 13, 1917, many specimens on cow in laboratory yard, H. P. Wood, collector; No. 8487, Olympia, Wash., December 28, 1918, on Jersey bull, R. W. Wells, collector; No. 8500, Uvalde, Tex., January 10, 1919, on calf, D. C. Parman, collector; No. 8995, Bennington, Vt., March 17, 1919, on cow, R. W. Wells, collector; No. 9699, Herkimer, N. Y., March 20, 1920, on calf, F. C. Bishopp, collector.

[1] ENDERLEIN, Günther. LÄUSE-STUDIEN . . *In* Zool. Anz., Bd. 28, No. 4, p. 144, fig. 14-15. 1904.

[2] FERRIS, G. F. CERVOPHTHIRIUS CRASSICORNIS. (N.) (ANOPLURA). *In* Ent. News, v. 27, no. 5, p. 197-200. 1916.

The species shows a marked tendency toward attaching in dense groups about the head and neck of the host. Sometimes these patches are almost circular.

In 1917 H. P. Wood made an effort to secure oviposition of the lice under control on cattle, but with little success. Evidence was gained which indicates that the incubation period is rather long, probably about 12 days, and also that the eggs will not hatch when removed from the host.

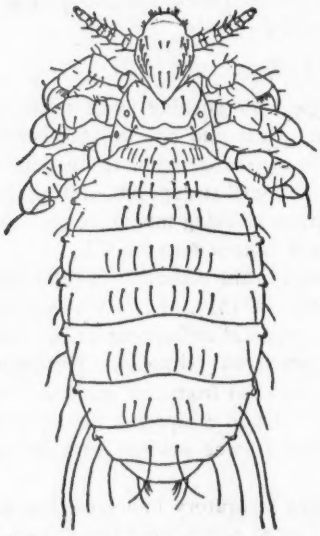

FIG. 1.—*Solenopotes capillatus:* Dorsal aspect of female. × 40.

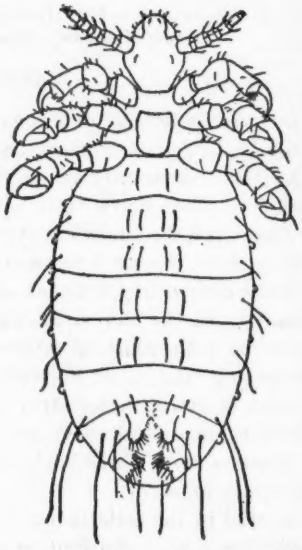

FIG. 2.—*Solenopotes capillatus:* Ventral aspect of female. × 40.

DESCRIPTION

THE FEMALE

As the female of this species has not been described, it will be characterized fully here.

Length (fig. 1 and 2) about 1.5 mm., greatest width about 0.7 mm., thorax and legs brownish yellow, abdomen grayish blue.

HEAD.—Length 287 μ, width 215 μ. Anterior margin rather broadly rounded, lateral margins slightly widest behind antennæ, somewhat narrowed at transverse groove just anterior to antennæ, posteriorly pointed. Antennæ attached about one-third length of head from anterior border, rostrum just ventrad of anterior margin, a chitinized rim around anterior margin above rostrum. Antennæ slightly longer than greatest width of head, basal segment markedly broader than succeeding segments, segments 3 and 4 somewhat shorter than others. Several short spines on anterior margin of head, two spines on ventral surface behind antennæ, dorsally with a slightly curved row of about five spines on either side, one somewhat smaller spine outside the anterior end of this row just in front of the antenna on either side, and two near the margin behind the antennæ. Near the median line is a small spine on either

side opposite the point of attachment of the antennæ and toward the posterior margin of the head another pair, somewhat longer than any others, about the same distance from the median line

THORAX.—About 200 μ long by 344 μ wide, deeply incised anteriorly to receive the head, narrowed somewhat anteriorly and with rounded sides. Division of thorax fairly distinct dorsally and the mesothorax and metathorax bearing at the margin a rather prominent but not projecting spiracle. Prothorax with two rather strong submedian spines and mesothorax with two or three small and one strong spine. Sternal plate about 172 μ long by 114 μ wide, not very highly chitinized, slightly narrow posteriorly, anterior end truncate, posterior end rounded.

LEGS.—Rather short and stout, anterior pair much shorter, more slender, and less chitinized than others. They terminate in long, slender claws, while the posterior legs are provided with highly chitinized dark reddish brown terminal segments and blunt claws. A few short hairs on all leg segments.

ABDOMEN.—Elongate oval, narrowing gradually to terminal segment which is broadly rounded; abdomen dorsally with a considerable number of yellowish, rather slender spines distributed as follows: First segment, two transverse rows, anterior with 8 or 10 spines irregular in length, posterior with from 4 to 6; second, from 4 to 6; third, 6; fourth, from 6 to 8; fifth, from 6 to 8; sixth, 8; seventh, 6; eighth, 2; the last rather longer than the others. Near the lateral margin of the second to seventh segments is a single spine on each side, those on the sixth and seventh being two or three times as long as the others and hairlike toward their tips. On the venter the spines are less variable in number than on the dorsum, the second to eighth segments with 4 submedian spines, the outer pair on second segment being small and those on the eighth segment being farther removed from the median line and very long and hairlike at tips. Near the lateral border on either side is a single row of spines on the third to seventh segments, those on the sixth and seventh segments being long (longer on the seventh) and hairlike toward the tips.

FIG. 3.—*Solenopotes capillatus*: Eighth and terminal segments of abdomen of female. × 53⅓.

On the posterior margin of the eighth segment are two genital flaps or protuberances margined with 7 rather stout spines (fig. 3). Between these on either side are 2 minute spines, and from the middle to the anterior border of this segment near the median line are 3 pairs of very short spines. The chitinized bands on the terminal segments are rather narrow dorsally and broad on their ventral margins. There is a slight projection on this band in the internal anterior angles which bears 3 or 4 stout spines on each side near the margin. Just anteriorly from the inner angles of the bands occur on each side a group of about 6 moderately stout spines, and mesad from their borders about 3 small spines.

The second to eighth segments are provided near their anterior margin with projecting, rather large spiracles 29 μ in diameter.

THE MALE

While Enderlein's [1] description of the male is fairly complete, it is deemed advisable to redescribe this sex and point out some of the variations in the distribution of the abdominal spines.

Length 1.2 mm., width 0.6 mm.

HEAD.—Length 287 μ, width 208 μ. Rather broadly rounded anteriorly (fig. 4), widest just behind antennæ which are attached about one-fourth of the length of the

[1] ENDERLEIN, Günther. op. cit.

head from the anterior margin. A row of about 6 small spines extending across near the anterior margin dorsally and a longitudinal row on each side with about 6 spines. One short spine in front and 2 behind each antenna and also 2 large spines toward posterior edge of head medially. Ventrally a spine of moderate length on each side behind and mesad of base of antennæ. Mouth parts slightly ventrad of anterior extremity, a chitinized transverse ridge running across the anterior margin just above the mouthparts.

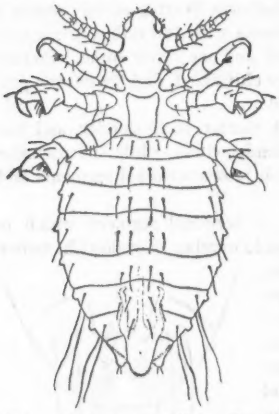

FIG. 4.—*Solenopotes capillatus*: Ventral aspect of male. × 40.

THORAX.—Much as in female, a few short and one long spine on either side of pronotum and mesonotum. Spiracles on pronotum and mesonotum prominent. Sternal plate more elongate than in female and slightly concave on lateral border.

ABDOMEN.—Greatest width at about fourth segment, elongate oval. Second to eighth segments provided with projecting spiracles as in female, ninth segment with a distinct notch on either side, the central terminal portion being rather stout and bearing a number of small spines along the border. On the dorsal side segments armed submedially as follows: The first segment with two transverse rows, anteriorly to these 6 small spines and posteriorly about 8 spines, the two median being the largest; second segment, 8 spines; third, 6 spines; fourth, 8 or 10 spines; fifth, 8 spines; sixth, 8 spines; seventh, 6 or 8 spines; eighth, from 4 to 6 spines. Near lateral margins another row of spines, one spine to each segment, those on seventh and eighth segments being very long and hairlike, those on first segment small. Ventrally, the second to seventh segments with a row of 4 spines submedially and the eighth with 2 spines. All ventral spines somewhat stronger than the dorsal ones. Near the lateral margin the second to eighth segments provided with a single spine on either side, those on seventh and eighth segments being long and hairlike, as on the dorsal surface.

Genital frame (fig. 5) rather simple, apparently consisting of six parts. Basal portion forked for about one-fifth of its length at the posterior end where it articulates with two elongate plates which in turn join at their posterior end with two other plates of slightly greater length. These diverge posteriorly and bend dorsally and cross the anterior ends of a wishbonelike plate the posterior end of which terminates in a rather acute, highly chitinized point known to some as the pseudopenis. The penis is simple, nearly equaling in length the inclosure of the frame, the aperture situated well back between the legs of the wishbonelike plate.

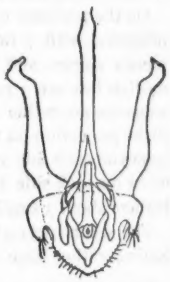

FIG. 5.—*Solenopotes capillatus:* Genital frame. × 106⅔.

NYMPHAL STAGES

First instar, color pale yellowish before feeding, except for parts of abdomen which are darker; after feeding, much as in adult though somewhat paler; tarsi and claws yellowish to light brown. Later instars darker.

HEAD.—Showing slightly stronger transverse groove than in adult.

THORAX.—About as in adult, but slightly less chitinized.

ABDOMEN.—In first instar very elongate, not wider than thorax; in later instar markedly broader, a shallow submarginal groove on each side running from first segment to about the seventh, where they join. Along the line of this groove on each side is a row of depressions, one near the anterior border of each segment. Spines about as in adult female though hairs are very short except on the sides of seventh and eighth segments on which they extend well beyond the tip of the abdomen. Apex of abdomen slightly bilobed, spiracles projecting distinctly on the third to eighth segments, inclusive.

THE EGG

Color pale yellowish. Elongate oval, the side next to the hair upon which attached practically straight, the other side curved, set at a comparatively small angle from the hair and cemented to it by a basal, somewhat heart-shaped, broad and comparatively short attachment (fig. 6). Length of egg, not including attachment, 735 μ, greatest width 278 μ at right angles to a plane passing through the egg and hair to which it is attached, the other diameter being about 244 μ. The well-defined, somewhat elevated operculum set almost at right angles to the straight side of the egg; diameter about 190 μ; its height about one-third of its diameter; length of attachment clamp about 190 μ, its greatest width about 180 μ. Surface of egg minutely reticulated, under moderate magnification giving a granular appearance. Operculum with a number of slight protuberances which give it a deeply roughened appearance.

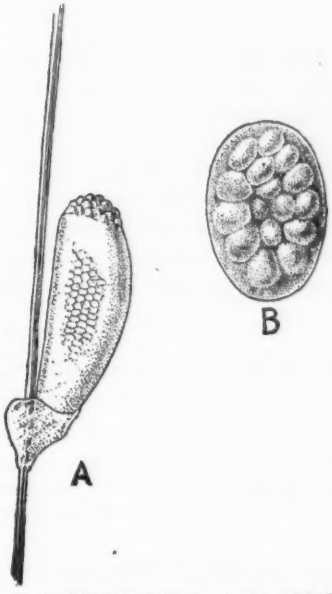

FIG. 6.—*Solenopotes capillatus:* A, Egg attached to hair, × 40; B, operculum of egg, greatly enlarged.

A number of eggs are frequently attached to a single hair and may be found anywhere from the base to the tip of the hair.

RATE OF CULM FORMATION IN BROMUS INERMIS

By L. R. WALDRON
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INTRODUCTION

Various investigators have made growth studies upon different organisms. Working with the rat, Donaldson[1] and other workers have published a number of formulas showing the growth of certain organs with respect mainly to the growth in body weight. The curves are mostly logarithmic in type. They are based on careful data and show the general trend of organic development relative to size of animal.

Pearl has made studies in growth phenomena and has developed curves to express the general type of growth. Working with Ceratophyllum,[2] he developed a logarithmic curve of the general type

$$Y = A + C \log (x - a)$$

which furnished a symbolical expression of the manner of growth dealing with rate of increase of leaves per whorl along the axis of the plant. He says:

> The mean number of leaves per whorl increases with each successive whorl, and in such a way that not only does the absolute increment diminish, but also the rate of increase diminishes as the ordinal number of the whorl measured from a fixed point increases.

In other words, this phase of growth is rather rapid at first and then slows down, both absolutely and comparatively.

Working with maize, Pearl and Surface[3] secured data upon height of plant which, from their previous studies, they were confident could be fitted with a logarithmic curve, probably of the type

$$Y = A + B \log x.$$

Here again the growth movement is rapid at first, but this rapidity decreases later. Pearl goes so far as to state that the growth of an organism can usually, if not always, be described by a curve of this type.

[1] DONALDSON, Henry H. THE RAT. REFERENCE TABLES AND DATA FOR THE ALBINO RAT (MUS NORVEGICUS ALBINUS) AND THE NORWAY RAT (MUS NORVEGICUS). 278 p., 31 charts, 89 tab. Philadelphia, 1915. References to the literature, p. 214-267, and references at end of chapters. Mem. Wistar Inst. Anat. and Biol., no. 6.

[2] PEARL, Raymond. VARIATION AND DIFFERENTIATION IN CERATOPHYLLUM. 136 p., 26 fig., 2 pl. Washington, D. C., 1907. Literature cited, p. 135-136. Carnegie Inst. Wash., Pub. 58.

[3] PEARL, Raymond, and SURFACE, Frank M. GROWTH AND VARIATION IN MAIZE. *In* Ztschr. Indukt. Abstam. u. Vererb., Bd. 14, Heft 3/4, p. 97-203, 15 fig. 1915. Bibliography, p. 171-172. Preliminary abstract *in* Proc. Nat. Acad. Sci., v. 1, no. 4, p. 222-226.

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In the work at hand, instead of a rapid increase in the early stages and then a falling off in size of increments, growth comes about by constantly increasing increments. It did not appear in the present study that the data were amenable to a logarithmic type of curve.

Blackman [1] has applied the compound interest law, commonly used by physicists, to plant growth, particularly to changes in weight undergone by annual plants from the germination stage to more mature stages. A fuller discussion of this law will be undertaken when the data have been presented.

CULM FORMATION IN BROMUS INERMIS

In the spring of 1916 a large number of seedlings of *Bromus inermis* Leyss were started in flats and later planted out in the field as individual plants 3.5 feet apart each way. The seed came from a Canadian source and was commercial seed. It had not been pedigreed or selected to any type. On June 19 countings were begun of the number of culms per plant of a limited number of plants.[2] At the time of first counting the plants had a height of 92.2 mm. as an average of the longest culm per plant, measuring to the extreme tip of the leaf. Stooling had begun on most of the plants. This consists essentially, in its earlier phases, in the formation and growth of additional culms springing from, at, or near the base of the primary culm. This study is concerned primarily with the rate of production of such secondary culms and the relation of their number to other characters of the plant.

Countings were made every five days except for the intervention of Sundays and holidays. The dates of the countings were June 19, 24, 29; July 5, 10, 15, 20, 25, 31; August 5, 10, 15, 22, 26, 31; September 5, 11.

There were thus a total of 17 countings, embracing a period of 85 days, including the dates of the first and last countings. At the time of the first counting the number of culms per plant [3] averaged 2.37, with a minimum of 1 and a maximum of 5. It is seen that at the first count growth was still in its earlier stages, from the standpoint of this study. At the date of the last count, September 11, culm formation was still in progress and apparently unaffected by weather conditions. The countings were stopped at this time, primarily because the large number of culms per plant made a precise count difficult.

The countings were continued over an interval of time sufficiently long so that the law of their rate of formation during favorable growth conditions can be deduced with a reasonable degree of satisfaction. A study of the rate of cessation of formation during the close of the growing

[1] BLACKMAN, V. H. THE COMPOUND INTEREST LAW AND PLANT GROWTH. *In* Ann. Bot., v. 33, no. 131, p. 353-360. 1919.

[2] Data were secured on 97 plants for the period of study.

[3] A culm was recognized as such when it had attained an extreme height of 25 mm., measurement being made from the tops of stakes driven down nearly flush with the surface of the ground.

season would be of interest but evidently of lesser importance than the problem at hand. In the one case the rate of formation of a turf is dealt with, while in the other case merely a minor phase of the problem would be studied, one relating to the behavior of the plant at the close of the growing season.

The raw data are not presented because of limited space. In Table I are presented the means, differences of the means, medians, and ranges for each date. The standard deviations, and consequently the coefficients of variation, were not calculated, as it was not seen that they would serve any useful purpose. It is obvious that the standard deviations and likewise the variations increase with great rapidity as the season progresses. Some of the plants stool with much greater rapidity than others, with the result that distances between the extreme limits constantly increase.

The means and medians were calculated by arithmetical methods. The data were almost necessarily left ungrouped, as the class units suitable for the earlier dates would be quite unsuitable for the later dates.

TABLE I.—*Means, medians, and extreme ranges of number of culms per plant of Bromus inermis at various dates*

Date.	Mean number of culms.	Difference of means.	Median.	Range.
June 19	2.37	.....	2.35	1 to 5
24	2.99	0.62	3.05	1 to 7
29	5.07	2.08	5.03	1 to 11
July 5	9.39	4.32	8.94	1 to 19
10	11.16	1.77	10.75	4 to 22
15	13.45	2.29	13.40	6 to 35
20	16.05	2.60	16.00	6 to 41
25	21.86	5.81	21.75	7 to 46
31	30.52	8.66	29.75	10 to 63
Aug. 5	35.11	4.59	34.38	12 to 78
10	43.55	8.44	42.75	17 to 107
15	53.72	10.77	51.25	21 to 133
22	68.46	14.72	65.00	24 to 171
26	77.74	9.28	73.00	24 to 214
31	89.57	11.83	82.75	32 to 254
Sept. 5	101.79	12.22	95.33	39 to 293
11	117.77	15.98	106.50	40 to 329

ANALYSIS OF TABLE I

From Table I one notes that the number of culms per plant increases with more or less irregularity from 2.37 at the time of the first counting to 117.77 on September 11, the date of the final count. This irregular advance may be ascribed in part to irregularities in moisture and temperature but to a considerable extent to the occasional variation of dates in counting. When the means are plotted, the irregularity due to the last-

mentioned cause may be made to disappear by arranging the abscissas in accordance with dates of counting.

For all countings except June 24 the median is smaller than the mean, and in these cases the skewness is presumably positive. Positive skewness may perhaps usually be presumed in cases of this kind. A certain number of plants progress slowly, while the values of the remainder are scattered over a wide range, but all in advance of the earlier stages. This is indicated by a study of the extreme ranges. The differences between the minimum values are much less than the corresponding differences between the maximum values.

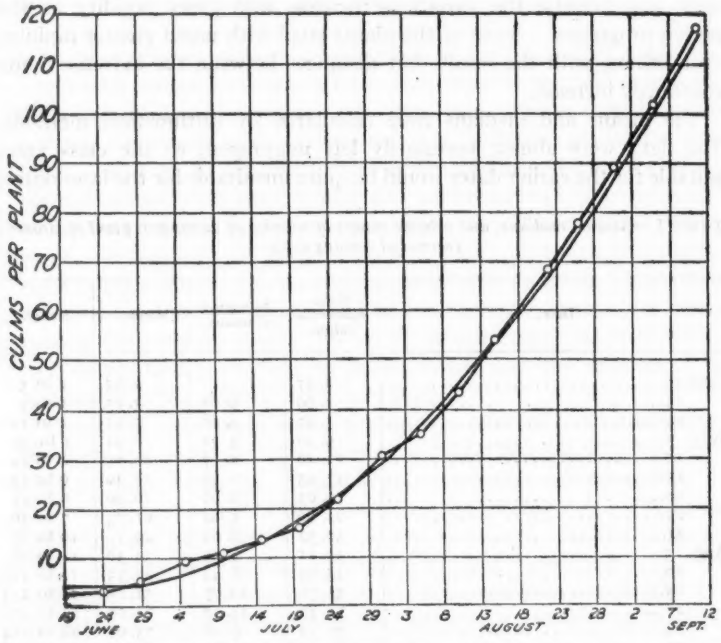


FIG. 1.—Plotting of average number of culms per plant at different dates of counting and curve fitted to the observations.

More interest centers about the discussion of the mean number of culms taken seriatim. To facilitate discussion these means have been plotted and are shown in figure 1 as the solid line. The abscissas in the figure for the observations are placed in accordance with the dates of counting, which are usually five days apart. The plotted observations show, on the whole, a very smooth series. From an inspection of the graph there is evidently something of a spurt in culm formation around July 1 and also a marked falling off around August 5. There were no obvious weather changes to account for these comparatively slight modifications from what one might consider the normal course of events.

DEVELOPMENT OF EQUATIONS

In order to give this series of observations a symbolical expression it will be necessary to develop an equation which, when plotted, will show a reasonable accordance with the observations. Such an equation was developed according to the method of moments developed by Pearson.[1] In the problem at hand there were 17, counting dates, and this gives us at once the odd number of classes required when this method is used. In working out the problem the first time the various counting dates were considered as natural numbers up to 17. The range would therefore be 1 to 17, or, in terms of the solution,

$$2l = 16, \text{ or } l = 8.$$

By this method of working the problem it is seen that the dates of counting are spaced at equal distances, when as a matter of fact occasionally 6 days (one instance each of 4 and 7 days) elapsed between two consecutive counting dates. To attempt a correction of this error the range was made coextensive with the entire counting period. The origin of x was taken at the middle counting date and extended 42 days both plus and minus. The table of corrective terms for moments of trapezia given by Pearson[1] had to be extended for values of L_1 and L_2, as l equaled 42 in this instance. This was easily done. Working the problem according to the first or non-weighted method, the following equation of a parabola of the second order was developed:

$$\text{(I)}\quad y = 40.313\left\{0.749029 + 1.405701\left(\frac{x}{l}\right) + 0.752914\left(\frac{x}{l}\right)^2\right\}.$$

The equation of a similar parabola developed according to weighted method was

$$\text{(II)}\quad y = 40.313\left\{0.749786 + 1.395915\left(\frac{x}{l}\right) + 0.750641\left(\frac{x}{l}\right)^2\right\}.$$

An attempt was made to fit parabolas of the third and fourth order by the non-weighted method, but with poor results. No attempts were made to fit parabolas of higher orders than the fourth.

Equations I and II are seen to be very similar, and both seem to give quite satisfactory fittings, equation II being perhaps appreciably better. There was a doubtful possibility that a better fit could be secured if a parabola of the third order, for instance, had been obtained by the method of weighting, but to secure this was not possible with the calculating machine at hand.

Equation II is fitted in figure 1 to the observations as shown by the curve with circles. Except for the two lower and four higher values of

[1] PEARSON, Karl. ON THE SYSTEMATIC FITTING OF CURVES TO OBSERVATIONS AND MEASUREMENTS. *In* Biometrika, v. 1, pt. 3, p. 265-303; v. 2, pt. 1, p. 1-23, 10 fig. 1902.

x this equation is appreciably better than equation I. However, for purposes of extrapolation beyond the upper range of observations, equation II may be considered the more conservative, as shown by the calculated results. The parabola obtained from equation I is very close indeed to the observations for the upper limits of the range, and perhaps this equation would give more accurate results for extrapolation purposes when calculations are made beyond the range. The extrapolated values would be the greater for equation I.

APPLICATION OF EQUATIONS

Assuming that either equation I or II is sufficiently correct for practical purposes, one may say that each represents or formulates the law of the rapidity of culm formation in *Bromus inermis* under the conditions indicated. These are: (1) Culm formation during the first or seedling year; (2) free from competition; and (3) under favorable soil and moisture conditions. The equations could, no doubt, be applied to certain other perennial grasses of similar growth with only slight modifications. Certainly they would need to be modified somewhat when applied to *Bromus inermis* grown under conditions other than those cited in this study.

These equations serve the purpose of indicating, at some future period for the plants under study, the amount of growth in number of culms produced, with all conditions remaining constant. It is true enough that conditions would not remain constant for any considerable future period for the reason that the season of seed maturity, for example, from the standpoint of the plant and the winter season of dormancy from the standpoint of environment intervene and profoundly modify culm formation.

It is a matter of value as well as of interest to compute the theoretical future rate of culm formation and see if there is any comparison within reason between the theoretical and the actual rates. Such a comparison might throw some interesting sidelights on the problem of deterioration of stand in brome-grass meadows.

EXTRAPOLATION

The method of extrapolation is simplicity itself, as one has merely to insert the proper value of x in the equations to secure the theoretical number of culms at any future period. The theoretical number of culms for a period of one year's steady growth will be found, and to do this x will have to be assigned the value of 322. This gives the number of culms at the specified time as 2,213, an increase of 2,097, or over 1,800 per cent, since the last actual count made September 11, 1916. An inspection of figure 1 indicates there would be a very rapid rate of increase after this date.

The areas of the 97 plants were computed from their diameters at the last counting date. At that time each plant occupied on an average 284.25 square cm. On the same basis the theoretical plants, after a year's steady growth, would cover an area of 5,244.241 square cm. Stated in diameters, the measurements would be 19.02 and 81.71 cm. in diameter, respectively, for the last counting date in 1916 and after the lapse of one year. The use of equation I would have increased the diameter of the theoretical plant only about 5 cm. It is worth noting that the plants discussed in this article were not far removed from the calculated size shortly after the beginning of the growing season in 1918. At that time the plants were still deficient about 1 dcm. or more in diameter from the theoretically estimated size. Assuming five months each season for rather rapid culm formation, it is evident that the given equations did not assume too much, provided culm formation proceeds the third season as rapidly as during the first and second seasons.

The foregoing does not imply, of course, that the number of culms during the third season was the number deducible from the equation. A plant may have a certain area at the close of the growing season. Such area will receive constant area increments during the next growing season. The original area also will be replenished with culms, but there is no precise knowledge at all as to the comparative number of culms for the two consecutive seasons upon the original area. Again, with certain plants, after the first season, deterioration begins within the original area, and such area of deterioration gradually enlarges. Within such an area the number of culms would be very evidently less than before deterioration began.

ANALYSIS OF CULM FORMATION

An examination of the data secured indicates that a closer analysis is possible than is given above. At the first count, as previously indicated, the plants fell into five groups in regard to number of culms. As but two plants had five culms, this group will be disregarded in the present analysis. There are thus left four groups constituted as follows:

CULMS PER PLANT.	NUMBER OF PLANTS.
1	28
2	24
3	28
4	15
Total	95

The mean was secured for each group for each counting date. The means of the four series are shown in Table II.

TABLE II.—*Means of number of culms per plant with initial culmage from 1 to 4*

Date.	Mean number of culms.			
	1	2	3	4
June 19				4.27
24	1.57	2.92	3.61	5.87
29	3.46	5.08	6.18	12.33
July 5	5.79	8.46	12.11	15.53
10	6.71	9.67	14.46	18.73
15	7.75	12.29	17.18	21.93
20	9.71	15.00	19.96	28.93
25	14.04	21.88	25.43	39.80
31	20.29	29.42	35.79	46.73
Aug. 5	24.39	32.58	41.18	58.27
10	31.50	39.63	52.29	68.00
15	38.18	49.21	65.39	86.60
22	48.18	62.83	83.71	97.47
26	54.32	71.67	95.43	109.60
31	63.86	83.63	109.07	123.93
Sept. 5	75.64	94.21	122.82	140.40
11	90.04	107.42	143.04	

A casual examination of the four series of means in Table II shows that, so far as number of culms per plant is concerned, there is a gradual increase in differences except between the two series initialing at 3 and 4. The series initialing at 4 has fewer culms per plant at the third and last count. Apparently the last series shows a lag, in comparison with what one observes among the first three series. A possible explanation of this lag will be given later, but attention is called again to the fact that the last series included only about half the number of plants found in the other series. To render the four groups more graphic they are plotted and shown in figure 2.

It seems strange at first sight that two groups of plants differing by only a single culm at an early stage of their existence should later come to show such a marked difference in this regard. It seemed possible that an explanation might be forthcoming on the basis of different degrees of heterosis; that is, the different degrees of growth vigor due to the differences in heterozygosis or amount of hybridity.

Two assumptions would be necessary, in connection with the well-known fact that brome grass is a normally inter-pollinating plant. One assumption would be that in a random sample of brome-grass seedlings some of them would possess a considerably higher degree of heterosis than others and that this difference in heterosis would result, in one direction, in a varying number of culms produced per plant. It is extremely probable that brome-grass seedlings taken at random have genotypes of sufficient diversity to be responsible for certain differences in vigor of growth which might easily find expression in a difference in number of culms. Moreover, one would look for an initial difference of this kind to be cumulative in character, as the difference in vigor would persist through the life history of the plant. The foregoing expla-

nation, while perhaps attractive, is rather too speculative for experimental proof.

The problem at hand is simply the explanation of the increasing difference in number of culms per plant for the various groups with different initial culmage, assuming, from lack of knowledge, that initial differences were purely accidental (enviromental) rather than genotypical.

If an explanation is at hand for the increasing diversity, starting from initial differences in the seedlings (environmental in character), there

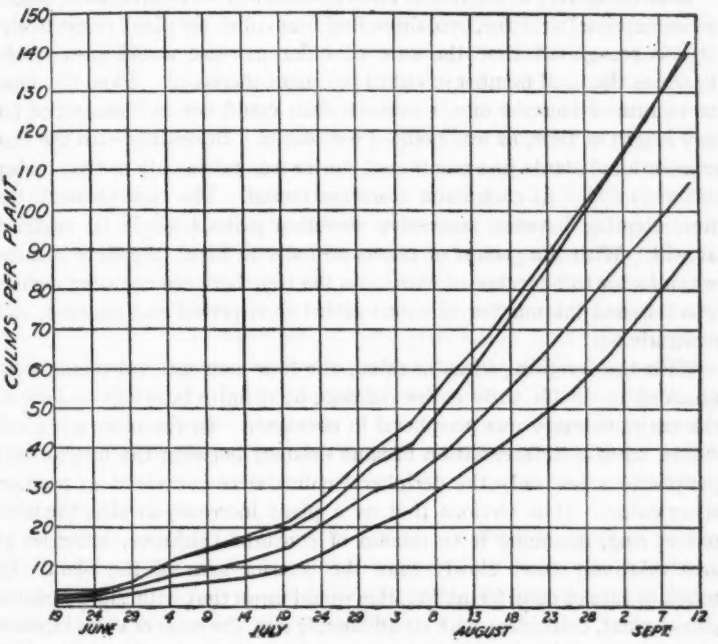


FIG. 2.—Plotting of average number of culms per plant at different dates of counting, arranged in four groups with regard to initial culmage.

would scarcely be room for additional explanations based on genotypical diversity.

In formulating another explanation, one may start with a general idea of the mechanics, let us say, of culm formation. For example, if a single culm is present, sooner or later an additional culm will be added, thus doubling the number. Later on the plant thus constituted will receive added increments, but the rate of increase of these future increments will to a considerable extent have to be assumed. However, it is certain that each culm, new and old, can not go on adding one more culm to itself indefinitely at each stage of culm accretion. Such a rate would soon be self-inhibiting from purely spatial considerations. Very

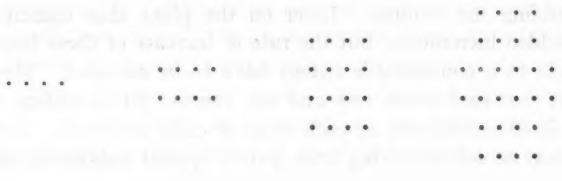
superficial observations lead to the necessary conclusion that culm formation in the interior of a grass plant, within the boundary of a more or less narrow peripheral ring, is sooner or later slowed down to a nearly zero rate. A few culms in the interior may be formed, but certainly anything like continued doubling is quite impossible. Culm increase is mainly always centrifugal in character.

USE OF CONVENTIONAL PLANTS

Relative merely to the rate of culm formation, four conventional plants were conceived with one, two, three, and four culms per plant, respectively. It was recognized that the rate of culm increase would presumably lessen as the total number of culms per plant increased. Even the minimum rate of increase of a 1-culmed plant could not be maintained for any length of time, as was pointed out above. In dealing with the four conventional plants just mentioned, notice was taken only of the number of culms added at each culm accretion period. The time element, the time elapsing between successive accretion periods, could be modified at will. With the groups of plants actually in hand, the time element was a factor to be reckoned with. As the time between counting periods was lessened the number of culms added each period was lessened, and contrariwise.

With the foregoing ideas in mind, the four conventional plants were assumed to double their entire culmage at definite intervals so long as the entire culmage was peripheral in character. In the more advanced states, when a differentiation became existent between the interior and peripheral areas, only the peripheral culms were conceived to produce sister culms. It is obvious that as a plant increases in size, the peripheral ring, assuming it to remain of constant thickness, increases in area relatively more slowly than the interior area of the plant. In terms of rate of culm formation, this would mean that with the increase in size of plant, coincident with its advancing age, the ratio of culm increase would constantly decrease as the total number of culms per plant increased.

The earlier stages of the conventional plant initialing with four culms is presented. This one suffices, since the plants initialing at one and two culms pass through the 4-culm stage. The plant initialing with three culms has its stages somewhat modified. Indicating culms by dots we have the following scheme:



From the foregoing explanation, it is seen that only the peripheral culms produce sister culms, and at any stage of increase a peripheral culm produces only one sister culm. The series resulting when the initial culmage is 4 is obviously as follows: 4, 8, 16, 28, 44, 64, etc., the first difference being continually augmented by 4. The general expression for this series is

$$y = 2x^2 - 2x + 4.$$

Now, the point in question is whether the results obtained in the field agree reasonably well with the figures obtained from the conventional plants. In the first place, one is dealing with the phenomenon of growth, which develops in a continuous manner. However, since the new growth is not recognized until it attains a certain stage of development in a culm of certain height, the accretions may be considered as being discrete in character. The method of recording the accretions, by counting, was necessarily discrete. The time elapsing between was chosen in a purely arbitrary manner, and in any explanation or symbolical description of rate of culm formation it would be purely a matter of choice if the length of time between countings were modified in one way or another. If the time periods were to be arbitrarily reduced from those used in the field, the number of culms appearing at each counting would have to be interpolated in so far as the new periods were concerned. The same would hold true if the time periods were increased unless, indeed, the new time periods were made some multiple of those actually used. As a matter of convenience, it seems better to double the period length between countings when comparing conventional plants with the actual ones. The number of countings would therefore be reduced to nine with an interval of about 10 days between successive counts.

In Table III are given the counts made upon the four series of plants based upon 10-day intervals, and for comparison there are presented the figures from the four conventional plants having a rate of culm increase according to the scheme outlined.

TABLE III.—*Comparison in rate of culm formation between four groups of plants and four conventional plants*

Date.	Number of culms.							
	A	B	A	B	A	B	A	B
June 19....	1	1	2	2	3	3	4	4
29....	3.46	2	5.08	4	6.18	6	5.87	8
July 10....	6.71	4	9.67	8	14.46	12	15.53	16
20....	9.71	8	15.00	16	19.96	22	21.93	28
31....	20.29	16	29.42	28	35.79	36	39.80	44
Aug. 10....	31.50	28	39.63	44	52.29	54	58.27	64
22....	48.14	44	62.83	64	83.71	76	86.60	88
31....	63.86	64	83.63	88	109.07	102	109.60	116
Sept. 11....	90.04	88	107.42	116	143.04	132	140.40	148

ANALYSIS OF TABLE III

It is evident from a casual inspection of Table III that there is a rather striking similarity between the two comparison columns, A and B, in the several cases.

Using either A or B as the standard, the deviations added with respect to sign give a sum equal to 5.11 culms for the entire number of counting periods. Reduced to the mean deviation for each counting period it is less than unity, an inconsequential amount. However, the size of the deviations must be considered; so that if they are added irrespective of sign and the mean deviation per group determined for each counting period, one finds the mean to be 2.92 culms. This mean deviation is about 6 per cent of the mean number of culms for each counting period. Considered from either of the foregoing standpoints, it appears that the agreement between the rate of culm formation of the real brome plants and the ideal rate of formation of the conventional plants is reasonably close. It is not to be understood that the plants in the field really follow the ideal method as outlined. This would be putting the case rather too strongly. It is known that the actual and conventional plants started with the same number of culms and that culm formation proceeds centrifugally in the actual plant as it does by hypothesis in the conventional plants. Finding the results in the two cases so closely in accord, one may say without much hesitation that given a certain number of groups of plants of *Bromus inermis* possessed of varying initial culmage, one may expect, with normal development, a continual increase in number of culms for each group but at the same time with a continual increasing diversity in number of culms between the various groups according to fixed rates.

While the correspondence of group A and group B, taking them as a whole, can be considered only general in character, it apparently is sufficiently close to make it seem unwise with our present knowledge to make other attempts to explain the increasing diversity in number of culms between the various groups with the advance of age of plants.

It should be observed that the number of plants in the group having four initial culms was somewhat lower than in the other groups. The lagging effect exhibited by this group may be attributed perhaps to the fact that the plants of the group did not comprise so representative a sample as did the plants of the other groups and that more than their due proportion lagged behind, thus diminishing the true mean. As a matter of fact there were a number of plants which behaved, after the first one or two counts, as though belonging genotypically to one of the groups having a smaller initial culmage. However, another explanation is possible. It may be that the effect of transplanting was more detrimental to the 4-culm plants, which were farther advanced, than to the plants not so far developed. Such an effect would be a retarding one and likely to be confused with constitutional difference.

COMPOUND INTEREST LAW

The compound interest law applied by Blackman[1] to plant growth deals with processes in which any rate of change varies as the quantity which is changed. This law evidently applies in the present case, as the larger the brome-grass plant the larger the peripheral ring which produces new culms. This law is expressed symbolically as

$$W_1 = W_o e^{rt}$$

where W_1 is the final weight or measure of the plant, W_o the initial weight or measure, r the rate of interest, t the time involved, and e the base of the natural system of logarithms. Obviously

$$r = \frac{\log W_1 - \log W_o}{t \log e}.$$

The rate of interest, r, appears to Blackman as an important physiological constant, for it represents to him the efficiency index of the plant as a producer of new material.

Similar efficiency indexes were calculated for culm formation in *Bromus inermis* for the four initial culmages for the various dates. Each index, or interest rate, indicates comparative average rate of growth per day for the period of growth to each respective date, using the proper initial culmage as the base in each of the four cases. The indexes are presented in Table IV.

TABLE IV.—*Efficiency indexes of culm formation with four-initial culmages as determined by the compound interest law*

Growth period.	One initial culm.	Two initial culms.	Three initial culms.	Four initial culms.
5	0.090	0.076	0.037	0.013
10	.124	.093	.072	.038
16	.110	.090	.087	.070
21	.091	.075	.075	.065
26	.079	.070	.067	.059
31	.073	.065	.061	.055
36	.073	.067	.059	.055
42	.072	.064	.059	.055
47	.068	.059	.056	.052
52	.066	.057	.055	.052
57	.064	.056	.054	.050
64	.061	.054	.052	.048
68	.059	.053	.051	.047
73	.057	.053	.049	.045
78	.056	.049	.048	.044
84	.054	.047	.046	.043

[1] Blackman, V. H. THE COMPOUND INTEREST LAW AND PLANT GROWTH *In* Ann. Bot., v. 33, no. 131, p. 353-360. 1919.

From Table IV one notes a distinct rise in the indexes up to the second or third counting period and then a gradual but somewhat irregular falling to the last period. The indexes as a whole decrease in size as the initial culmage increases. For the group of plants initialing at 4 the efficiency index, or rate of interest, averages less and is uniformly less than for any of the other groups. During the early stages the rate of increase is considerably higher with the plants with fewer culms. An individual plant with 1 culm doubles its culmage at the first increase, but with a 4-culmed plant the culmage need be increased but by 25 per cent. It would seem to appear in this case that the plants with the larger initial culmage are less "efficient" than the smaller initialing group and that this diminished "efficiency" is automatically due to the larger size of plant. This condition is quite different in those cases cited by Blackman, where the small initial seed weights lead directly to a lessened efficiency index. It is not evident that the indexes dealing with culm formation in brome grass have any real organic significance.

SUMMARY

A study is made of rate of culm formation in *Bromus inermis*. The rate of increase is not fixed but takes place at an accelerating rate. An equation was developed which expresses the rate of increase in a symbolical manner. The resulting curve is of the parabolic type.

An analysis of the data shows that plants initialing at culmage 1, 2, 3, and 4 become, on the whole, increasingly more divergent in number of culms during the season. This increasing divergence may be explained from the initial culmage and the consequent mechanics of further culm formation. It is not evident that the compound interest law has any real organic significance when applied to culm formation in *Bromus inermis*.

RELIABILITY OF THE NAIL TEST FOR PREDICTING THE CHEMICAL COMPOSITION OF GREEN SWEET-CORN[1]

By CHARLES O. APPLEMAN

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INTRODUCTION

The chemical composition of green sweetcorn changes very greatly during the ripening period. The rate at which these changes occur depends upon the prevailing temperature. In warm weather the stage of ripening that furnishes the most desirable chemical composition of green sweetcorn, either for table use or packing into cans, passes very quickly. This rapidly changing composition of the corn also introduces the chief difficulty in conducting various lines of experimental work that require the sampling of ears as nearly as possible at the same stage of ripening. In practice, as well as in experimental work, it has been customary to resort to inspection of certain physical and structural characters of the corn as a basis for the prediction of the approximate chemical composition of the kernels. One of the tests frequently used in this connection, especially in experimental work, is the so-called nail test.

THE NAIL TEST

In the manipulation of the nail test the thumb-nail is thrust into the kernel, and if the exudate is milky the corn is said to be in the milk or best edible stage. If, on the other hand, dough is forced out of the kernel by the nail the corn is said to be in the dough stage and is considered too far advanced in ripening to give the best quality to green corn. In order to determine within what limits the chemical composition of the corn can be predicted by the nail test, it was applied at different stages of ripening, and samples were taken from the ear for analyses. In this study four stages were indicated by the nail test and designated as follows:

(1) The premilk stage. The exudate from the kernels in this stage is cloudy or opalescent, but not white and milky.

(2) The typical milk stage. The exudate is milky, and the kernels are white.

(3) The early dough stage. In this stage a little pressure by the nail is required to force out the creamy contents, which also contain a little dough.

[1] Published with the approval of the Director of the Maryland Agricultural Experiment Station.

A large part of the experimental data in this paper was compiled from other problems, in which both John M. Arthur and S. V. Eaton, former assistants in this laboratory, contributed to the analytical work.

(4) The dough stage. At this stage of ripening only dough is force out of the kernels by the nail, and the kernels are also beginning to show considerable yellow color.

EXPERIMENTAL DATA

Stowell's Evergreen corn furnished the material for this study, which covered two crops. The first crop was planted so that it ripened in August. The average hourly mean temperature for the ripening period was 83° F. This crop will be spoken of as the early crop. The second crop ripened in the cool autumn. The average hourly mean temperature for the ripening period was 65°. Besides being cool, the weather was usually cloudy and damp. This crop of corn will be designated as the late crop.

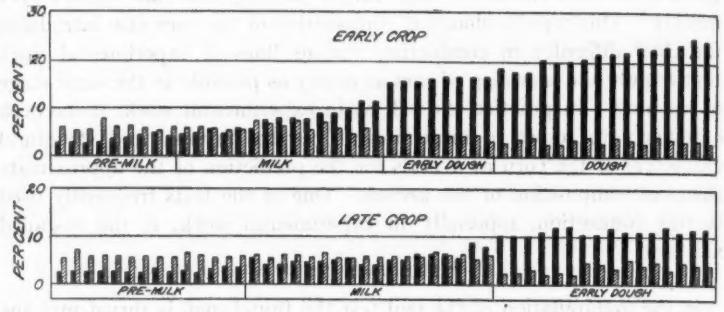

FIG. 1.—Relative percentages of total sugars and starch in green sweetcorn at different stages of ripening as indicated by the nail test. The solid columns represents the starch percentages, and the broken columns the percentages of total sugars. Each pair of columns represents a single ear. The ears for each stage of ripening are arranged according to the percentage of water in the kernels, beginning with the highest water content at the left of the figure.

The experimental results are set forth in Tables I, II, and III and in figure 1. Only moisture and carbohydrate determinations are given, as these constituents are the ones chiefly involved in the changes in percentage composition of the corn during ripening.

TABLE I.—*Percentage composition of sweetcorn at different stages of ripening as indicated by the nail test. Early crop*

Nail test.	Number of tests.		Moisture.	Total sugars.	Starch.	Ratio of sugar to starch.
Premilk	9	Maximum	87.52	8.06	4.93	1.903
		Minimum	83.01	5.15	2.33	
		Average	85.10	6.26	3.29	
Milk	18	Maximum	84.94	7.56	11.94	.750
		Minimum	73.25	4.08	4.27	
		Average	80.16	5.79	7.72	
Early dough	9	Maximum	73.50	4.61	19.57	.239
		Minimum	66.24	2.94	15.15	
		Average	71.07	3.91	16.35	
Dough	18	Maximum	69.59	4.17	25.42	.146
		Minimum	58.76	2.12	17.80	
		Average	63.92	3.17	21.62	

TABLE II.—*Percentage composition of sweetcorn at different stages of ripening as indicated by the nail test. Late crop*

Nail test.	Number of tests.		Moisture.	Total sugars.	Starch.	Ratio of sugar to starch.
Premilk	14	Maximum	90. 58	6. 78	3. 56	2. 126
		Minimum	85. 51	5. 21	2. 14	
		Average	88. 75	5. 76	2. 71	
Milk	16	Maximum	85. 40	6. 68	8. 73	1. 054
		Minimum	80. 56	5. 02	3. 89	
		Average	83. 54	5. 81	5. 51	
Early dough	16	Maximum	82. 56	4. 93	12. 66	. 300
		Minimum	74. 13	1. 58	10. 19	
		Average	77. 95	3. 38	11. 24	

TABLE III——*Average percentages of Tables I and II calculated to dry basis*

Crop.	Premilk stage.		Milk stage.		Early dough stage.		Dough stage.	
	Total sugar.	Starch.	Total sugar.	Starch.	Total sugar.	Starch.	Total sugar.	Starch
Early	42. 013	22. 080	29. 183	38. 911	13. 515	56. 519	8. 786	59. 922
Late	51. 200	24. 080	35. 297	33. 475	15. 328	50. 975	.....	.....

EARLY CROP

The percentages of moisture, total sugar, and starch were fairly uniform in the kernels from the ears of the early crop classified by the nail test as being in the premilk stage. The same was true of the ears picked in the early dough stage. The ears picked when the nail test indicated the typical milk stage showed, however, a considerable range in the percentages of the foregoing constituents, indicating extensive carbohydrate transformation in the kernels during the milk stage. The ratios of total sugar to starch ranged from 1.428 to 0.387.

During the period when the corn gave the typical dough test the percentages of starch gradually increased. The percentages of total sugar were somewhat irregular but uniformly low. The dough stage covered the period from the end of the early dough stage until the moisture in the kernels was reduced to about 60 per cent. At this point the carbohydrate transformations had practically reached equilibrium positions, and thereafter the percentages of sugars and starch increased only as water was lost by evaporation. Calculated on wet basis, the percentages of total sugar for each stage of ripening showed less variation than the percentages of starch.

LATE CROP

The percentage composition of the kernels for each stage of the late crop was much more uniform than the corresponding stage of the early crop. The percentages of starch in both the milk and early dough stages

were lower in the late crop than in the early crop. The ripening processes proceed to nearly equilibrium positions independently of the rate of water loss by evaporation. On account of the cool, damp weather, the late crop came to the early dough stage with a relatively high percentage of water, making the percentage of starch lower than at the same stage in the early crop. By comparing the percentage of total sugar and starch based on dry weight and also the ratios of total sugars to starch, it will be noted that the late crop in the milk and early dough stages was not quite as far advanced in ripening as the early crop in the same stages. A smaller ratio of sugar to starch indicates a more advanced stage of ripening.

SUMMARY AND CONCLUSIONS

Based upon the nail test the ripening period of sweetcorn was divided into four stages—the premilk, typical milk, early dough, and dough stages. The application of the nail test in classifying green corn into these four stages of ripening is described.

The reliability of the nail test as a means of predicting the chemical composition of green corn at different stages of ripening is shown by the results of chemical analyses of the corn after the nail test was applied.

The reliability of the nail test is influenced by the rate of ripening and also by the rate of water loss by evaporation.

The corresponding stages of crops ripening under different climatic conditions vary both in uniformity of composition and average percentage composition. The percentage composition of the carbohydrates in the milk stage of a late crop was much more uniform than in the same stage of an early crop.

The nail test is most reliable when applied to crops which ripen slowly in the cool autumn. These crops are most suitable for experimental work requiring the sampling of ears as nearly as possible at the same stage of ripening.

In each of the ripening stages except the dough stages the percentage of total sugar was more constant than the percentage of starch.

As ripening proceeds, the increase in the percentage of starch is much greater than can be accounted for by the decrease in the percentage of sugars. From the beginning of kernel formation until the end of the ripening period there is a continual movement of sugar from the plant into the kernels, where it is transformed into starch.

TRANSMISSION OF SOME WILT DISEASES IN SEED POTATOES[1]

By M. B. McKay

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Among the diseases of the potato plant (*Solanum tuberosum* L.), the wilt diseases are the most widely known and are reported to cause the greatest loss the whole country over. There are several fungi which cause wilt of potato plants, but the most important and most frequently mentioned are *Fusarium oxysporum* Schlecht. and *Verticillium albo-atrum* Reinke and Berthold. These parasites have been known for many years as a cause of disease in potatoes, and although many important facts concerning their nature and control have been learned by the different investigators who have studied them, there still remain points of interest and value concerning which there is a lack of adequate and definite knowledge and which will require much additional work to be completely cleared up. The investigations reported here were begun in order to secure some knowledge of the importance of these wilt diseases in Oregon and to determine the extent to which the fungi causing them are transmitted from year to year in seed potatoes. *Fusarium radicicola* Wollenw. has during this work been frequently isolated from the stem-end vascular region of potato tubers that in appearance could not be distinguished from those affected by a known wilt fungus. It has been necessary, therefore, to include this fungus in this study even though it is not known to be a cause of wilt of potato plants. Incidentally, also, some data have been collected on the natural occurrence of these organisms in the soil.

This work was begun in 1916 and continued to the end of 1920. It has been conducted mainly in the vicinity of Corvallis, though field observations have shown that the organisms studied performed in very much the same way throughout western Oregon. However, the results secured probably could not apply in their entirety to the eastern part of the State where the soil, climatic, and other conditions are very different. The work was begun with the supposition that *Fusarium oxysporum* was the organism chiefly responsible for potato-wilt in this region, but as the investigation has progressed it has been found that *Verticillium albo-atrum* is much the more serious of the two and that the former organism is relatively unimportant in western Oregon. Some of the tests begun for the purpose of determining the length of rotation necessary to avoid wilt infection from the soil can not be completed before a few more seasons of study. The work on the transmission of the organisms in seed potatoes has been terminated, however, and the results secured are given here.

[1] Published with the permission of the Director of the Oregon Agricultural Experiment Station.

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TRANSMISSION OF ORGANISMS IN SEED POTATOES

MATERIALS AND METHODS

In 1916 several lots of diseased and healthy potatoes of different varieties and from several localities were secured as follows: Seven lots of diseased potatoes—one each of American Wonder, Burbank, Early Rose, Up-to-Date, and Producer from three localities in Oregon; one lot of Rural New Yorker from Colorado; and one lot of Sir Walter Raleigh from Michigan; and six lots of healthy potatoes—one each of Burbank, Uncle Sam, and Gold Coin from Oregon, and one each of Burbank, Rural New Yorker, and Irish Cobbler from Wisconsin. These tubers were tested for the presence or absence of organisms in the stem-end vascular region in the following manner: The potatoes were weighed, numbered, washed, treated with mercuric chlorid 1 to 1,000 for two hours, rinsed through two lots of boiled and cooled water, spread out for one day in the laboratory to dry, placed in clean paper bags, and later cultured as follows: With a flamed and cooled scalpel a small cone of tissue about ½ inch in diameter and ⅛ inch deep was removed from around the point of stolon attachment. With another flamed and cooled scalpel a piece of the inner exposed vascular tissue, together with some surrounding parenchyma tissue, was taken from the discolored area (Pl. 139, A, B) when present, or from apparently normal tissue when discoloration was not present. This was placed in a test tube containing a moist sterilized sweet clover stem and incubated in the laboratory exposed to strong north light. As a rule a pure culture of whatever organism was present was secured (Pl. 141, B), though occasionally more than one organism was isolated. These organisms could often be identified directly from the original isolation culture, though always in the case of *Fusarium* spp. transfers were made to tubes of sweet clover stems, steamed potato cylinders, and steamed rice for final identification. By means of growth characters, colors, and characters of the spores which developed on these media, many of the species, including *F. oxysporum*, *F. radicicola*, *F. solani* (Mart.) Sacc., *F. discolor* App. and Wollenw., *F. discolor* var. *sulphureum* (Schlecht.) App. and Wollenw., *F. coeruleum* (Lib.) Sacc., and *F. culmorum* (W. G. Sm.) Sacc. could be determined by the methods of Wollenweber (13)[1] and Carpenter (*2*). Occasionally other species of Fusarium were encountered with which the author was not familiar and which were not determined.

After taking cultures the tubers were then prepared for planting. All tubers weighing 3 ounces or less were planted whole; those weighing from 4 to 7 ounces, inclusive, were divided into two lots, one lot being cut transversely into stem and eye halves and the other longitudinally into right and left halves; and those weighing 8 ounces and over were cut longitudinally and transversely into quarters (Pl. 139, C). All

[1] Reference is made by number (italic) to "Literature cited," p. 847-848.

the seed pieces were then planted on recently cleared land which had never grown a crop of potatoes and were given good care throughout the growing season. During the season notes on vine growth were made at occasional intervals. In the fall all the hills were dug and weighed separately. All hills grown from seed pieces from which known or suspected parasitic organisms had been isolated and a representative number of hills grown from fungus-free seed pieces as indicated by the cultures were kept for culturing in the same way that the seed tubers had been cultured in the spring. Some of this material was then kept for use as seed stock the following season, when a much larger planting on well-rotated land was made. The results obtained during the different seasons did not vary greatly but appeared to be in close accord.

RELATION BETWEEN TUBER SYMPTOMS AND OCCURRENCE OF ORGANISMS THEREIN

The presence or absence of discoloration in the vascular region of the stem end of potato tubers has rather generally been taken (*5*, *7*) as a reliable guide to the presence or absence of wilt-producing fungi, though for *Verticillium albo-atrum*, Pethybridge (*8*) has pointed out that this is far from being an infallible sign. Based on a study made in 1915 and with which the writer was associated, Edson (*4*) states that—

> In the materials studied, vascular discoloration of the stem-end tissues of Irish potato tubers was not found to be proof of the presence of parasitic fungi. Discolored bundles were often sterile, and fungi were frequently isolated from tissues which appeared normal.

The extent to which the presence or absence of discoloration can be depended on as a guide to the presence or absence of wilt-producing fungi is of importance, for it is frequently desirable to estimate the amount of wilt infection in seed potatoes merely from the appearance of the tubers. Consequently, a further study has been made of this relation in several different lots of potato tubers, of which the following may be mentioned in detail:

Six hundred Up-to-Date tubers grown in 1917 in hills attacked by *Verticillium albo-atrum* were cultured by the method outlined above. Nearly three-fourths of them (439 tubers, or 73.2 per cent) yielded *V. albo-atrum* in culture. Of these, 70.8 per cent were "browned" in the vascular region at the stem end, 19.6 per cent were "yellowed," and 9.6 per cent were "not discolored" at all. Of the 95 tubers in this lot which gave no organism in culture, 18.9 per cent were "browned" in the vascular region, 17.9 per cent were "yellowed," and 63.2 per cent were "not discolored." There were 111 tubers altogether which had no discoloration in the vascular region. Of these 54 per cent gave no organism in the cultures; 8.1 per cent gave "miscellaneous fungi" to which no importance can be attached, for they probably cause no disease of potatoes; while more than a third, 37.9 per cent, gave *V. albo-atrum*.

Of all the tubers which were "browned," 14.2 per cent gave no organism of importance, and 84.3 per cent gave *V. albo-atrum*. Thus, if this lot of tubers had been sorted for seed on the basis of the presence or absence of discoloration in the stem-end vascular region, 38 per cent of those passed as fit for seed would have been infected with *V. albo-atrum*, while 14 per cent of those eliminated for seed purposes would apparently have been entirely free from a wilt-producing organism.

In another lot of 647 tubers of seven varieties grown in 1917 from disease-free seed potatoes on soil badly infested with *Verticillium albo-atrum*, nearly half of them, or 293 tubers, were "browned" in the vascular region. These when cultured gave 55.3 per cent *V. albo-atrum*, 21.5 per cent *Fusarium radicicola*, 14.7 per cent "miscellaneous fungi," and 7.2 per

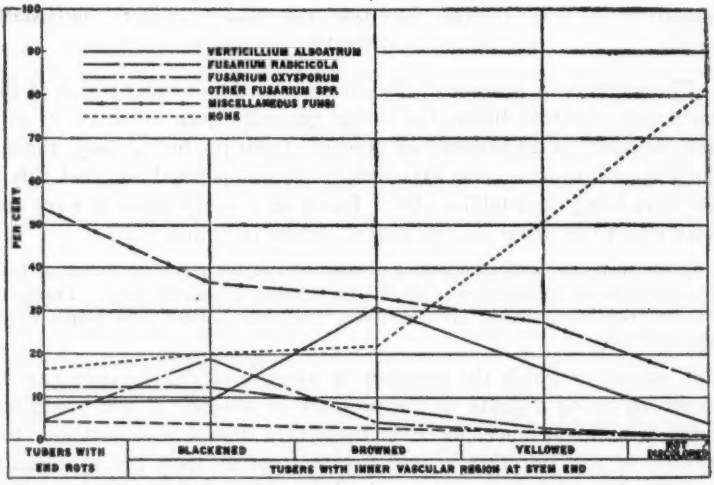

FIG. 1.—Diagram prepared from the vertical percentages given in Table I, showing the percentage occurrence of different organisms in tubers of a given discoloration.

cent no organism. Of the 260 tubers of the entire lot which gave *V. albo-atrum* in cultures, 2.7 per cent were affected by "jelly end" or slight stem-end rots, 1.9 per cent were "blackened" in the stem end, 62.3 per cent were "browned," 30.4 per cent were "yellowed," and 2.7 per cent showed "no discoloration" in the vascular region.

In another lot of 498 potato tubers of seven varieties grown in 1917, from disease-free seed potatoes inoculated at planting time with pure cultures of *Verticillium albo-atrum*, 232 tubers were "browned" in the vascular region. These when cultured gave 60.5 per cent *V. albo-atrum*, 9.6 per cent *Fusarium radicicola*, 26.5 per cent "miscellaneous fungi," and 2.1 per cent no organism. Of the 244 tubers which gave *V. albo-atrum* in cultures, 0.8 per cent were affected by "jelly end" or slight dry stem-end rots, 2.9 per cent were "blackened" in the vascular region,

82.4 per cent were "browned," 13.5 per cent were "yellowed," and only 0.4 per cent were "not discolored."

In still another lot of 258 Up-to-Date potato tubers grown by plants wilted naturally in the field with *Verticillium albo-atrum* during the season of 1916, 75 were "browned" in the vascular region. These when cultured gave 57.3 per cent *V. albo-atrum*, 9.3 per cent *Fusarium* spp., 28 per cent "miscellaneous fungi," and 5.3 per cent no organism. Of the 97 tubers which gave *V. albo-atrum* in cultures, 44.3 per cent were "browned" in the vascular region, 41.2 per cent were "yellowed," and 14.4 per cent were "not discolored."

In Table I is given a summary of practically all of the data collected during the course of this investigation on the relation of discoloration

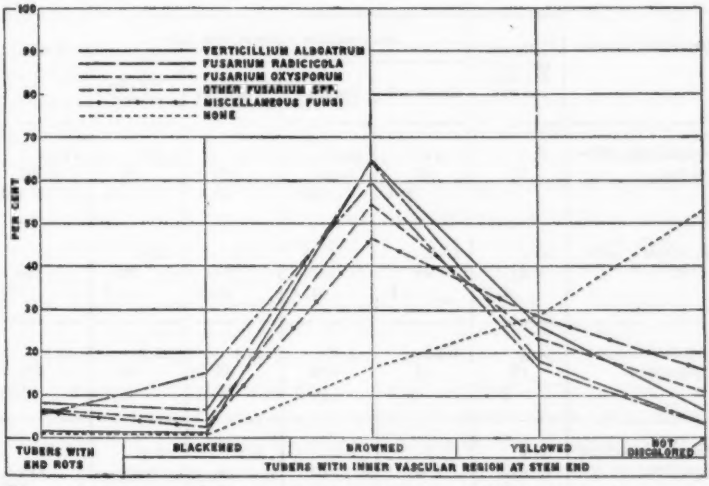

FIG. 2.—Diagram prepared from the horizontal percentages given in Table I, showing the percentage occurrence of a given organism in tubers of different discolorations.

of the vascular region to the occurrence of organisms in potato tubers. A part of the data in the table is shown graphically in figures 1 and 2. The results shown here are from a total of 12,136 tubers grown under a variety of conditions during three seasons from nine varieties and should therefore not be unusual but should serve as a basis for seemingly reliable conclusions. The table shows that *Verticillium albo-atrum* was isolated from 2.097 tubers, of which only a small percentage, 1.5, were affected by "jelly end" and slight dry stem-end rots. This is considered to be an accidental and mixed rather than a specific infection, because the great majoirty of the tubers affected by such rots gave other organisms in culture and all available data point to the fact that *V. albo-atrum* does not cause a specific rot of potato tubers. Also, only a small percentage, 1.1, were "blackened" in the vascular region. The

great majority of the tubers, 64.6 per cent, were "browned"; a large portion, 26.2 per cent, were "yellow" while a comparatively small though appreciable number, 6.6 per cent, were "not discolored." Thus the data indicate that this fungus when present in potato tubers is accompanied in the majority of cases by distinct discoloration but that frequently the discoloration is very light or even entirely absent and that therefore discoloration of the tubers is not a reliable basis for judging whether or not this fungus is present.

TABLE I.—*Relation between stem-end vascular-tissue discoloration and occurrence of organisms in potato tubers grown during the seasons of 1915, 1916, and 1917, under various conditions, some by diseased and others by healthy plants*[a]

Organisms isolated.	Tubers with—					Totals.
	"Jelly-end" and slight dry stem-end rots.	Inner vascular region at stem end—				
		Blackened.	Browned.	Yellowed.	Not discolored.	
Verticillium albo-atrum.	8.8 31 1.5	9.1 22 1.1	30.7 1,355 64.6	16.5 550 26.2	3.6 139 6.6	17.3 2,097 100
Fusarium radici-cola.	12.2 43 8.3	12.1 29 5.6	7.5 331 64.2	2.8 94 18.2	0.5 19 3.7	4.2 516 100
Fusarium oxy-sporum.	4.5 16 5.4	18.8 45 15.2	4.0 176 59.7	1.4 48 16.3	0.3 10 3.4	2.4 295 100
Other Fusarium species.	4.2 15 6.9	3.7 9 4.1	2.7 119 54.3	1.6 52 23.7	0.7 24 11.0	1.8 219 100
Miscellaneous fungi.	53.9 191 6.1	36.3 87 2.8	33.2 1,463 46.4	27.2 906 28.7	13.3 506 16.0	26.0 3,153 100
None.....	16.4 58 1.0	20.0 48 .8	21.9 969 16.5	50.5 1,680 28.7	81.6 3,101 53.0	48.3 5,856 100
Totals.....	100 354 2.9	100 240 2.0	100 4,413 36.4	100 3,330 27.4	100 3,799 31.3	100 12,136 100

[a] In each box the middle set of figures shows the number of tubers which in culture gave the results indicated in the headings of the intersecting columns; the lower right set of figures gives the percentage this number is of the total tubers represented in the horizontal column; and the upper left set gives the percentage of the total tubers in the vertical column.

Fusarium radicicola was isolated from 4.2 per cent of all the tubers cultured and included in the table. It occurred to a greater extent than *Verticillium albo-atrum* in the "endrot" and "blackened" tubers, the percentages for *F. radicicola* being 8.3 and 5.6, and for *V. albo-atrum* 1.5 and 1.1, respectively; and much less in the "yellowed" and "not discolored" tubers, the percentages being 18.2 and 3.7 for the former fungus, and 26.2 and 6.6 for the latter, respectively. The majority, 64.2 per cent, of the tubers which gave this fungus were "browned" in the vascular region. From these figures it must be concluded that this fungus occurs rather frequently in potato tubers and that it causes a somewhat heavier discoloration than *V. albo-atrum* in the invaded tissues. This latter fact is well shown in figure 2, in which at the left of the center, where the results from the heavily discolored tubers appear, *F. radicicola* occupies a higher position than *V. albo-atrum*, and at the right of the center, where the results from the lightly discolored tubers are given, it occupies a lower position than *V. albo-atrum*.

Fusarium oxysporum has not been isolated during the course of this investigation as frequently as either of the other two organisms already mentioned, having been secured from 295 tubers, or only 2.4 per cent of all the tubers cultured. Fifteen and two-tenths per cent of the tubers from which this fungus was isolated were "blackened" and only 3.4 per cent were "not discolored," as compared to 5.6 per cent and 3.7 per cent, respectively, for *F. radicicola* and 1.1 per cent and 6.6 per cent, respectively, for *Verticillium albo-atrum*. A smaller percentage of the tubers from which *F. oxysporum* was isolated were "browned" than was true of those from which *F. radicicola* and *V. albo-atrum* were secured, the percentages being 59.7 as compared to 64.2 and 64.6, respectively. Thus it appears that *F. oxysporum* caused even heavier discoloration in the tubers than either of the other two organisms. Although this is contrary to statements that are often made in literature (5, 7), the results secured during the course of this investigation have been consistent on this point throughout, and it is believed that they are quite representative of the facts.

Several determined and undetermined species are grouped in Table I under "other Fusarium species," some of which may be mentioned on account of their economic importance. *Fusarium trichothecioides* Wollenw. was isolated in April, 1916, from one tuber which was "browned" in the stem-end vascular region. There was no rot present in this tuber, although other tubers in the same lot were affected by "powdery dryrot" and presented the typical appearance of this disease. One stem-end seed piece from this "browned" tuber produced a normal plant, but the organism appeared in two tubers out of nine produced in the hill, one of which was affected the following spring by typical powdery dryrot, while the other was "blackened" in the stem-end vascular region though not rotted. The discoloration present in this "blackened" and the

former "browned" tuber could not be distinguished in any way from that usually present in tubers affected by *Verticillium albo-atrum* or *F. oxysporum*. *F. discolor* was isolated once from a tuber that was "blackened," eight times from "browned" tubers, and twice from "yellowed" tubers; *F. discolor* var. *sulphureum* once from a "browned" and once from a "yellowed" tuber; *F. culmorum*, twice from "browned" tubers, and *F. solani* once from a "browned" and twice from "not discolored" tubers. A rather large number, 11 per cent of these "other Fusarium species" caused no discoloration in the affected tubers, though the largest portion of them, 54.3 per cent, were present in "browned" tubers.

Under "miscellaneous fungi" are grouped all other organisms secured in the culture series. These are, so far as known, nonparasitic, with a few exceptions. *Colletotrichum solanicolum* O'Gara was isolated from 1 "blackened," 12 "browned," 2 "yellowed," and 2 "not discolored" tubers. Rhizoctonia (*Corticium vagum* B. and C.) was isolated from 6 tubers having stem-end rot, 3 of which were dry and 3 moist and rather soft, and from 8 "browned" and 1 "yellowed" tubers. *Spondylocladium atrovirens* Harz was isolated from 1 "browned," 1 "yellowed," and 2 "not discolored" tubers. The miscellaneous fungi isolated from potato tubers varied considerably from year to year, sometimes one and sometimes another predominating. So many cultures of *Naemosphaera* sp. were secured from the tubers grown one year, usually from distinctly "browned" tubers, that this organism was suspected of being parasitic. Inoculation tests, however, gave negative results. The longer the potatoes were kept in storage the larger was the number of saprophytic organisms which they gave in cultures. Some of the additional miscellaneous organisms isolated may be indicated by the generic names only—*Acremonium*, sp., *Alternaria*, sp., *Botrytis* sp., *Cephalothecium* sp., *Cladosporium* sp., *Chaetomium* spp. (2), *Helminthosporium* sp., *Mucor* sp., *Penicillium* spp. (2), *Periola* sp., *Pestalozzia* sp., *Phoma* sp., *Ramularia* sp., *Sclerotinia* sp., *Sporotrichum* sp., *Stemphyllium* sp., *Stysanus stemonitis* (Pers.) Corda, *Vermicularia* sp., *Verticillium cinnabarinum*, Reinke and Berth, and *Zygodesmus* sp. While some of these organisms may have entered sometimes as contaminations in the cultures, most of them had penetrated at least slightly into the tissues of the stem end of the tubers, usually causing some discoloration there. Seventy-five per cent of these tubers were "browned" or "yellowed," and about 9 per cent were "blackened" or had "endrot," and only 16 per cent were "not discolored."

The percentage distribution with respect to the recorded stem-end discoloration of the tubers from which "no organisms" were secured is in considerable contrast to the low percentages of "no discoloration" and the high percentages of distinct coloration in the tubers from which the different classes of organisms, as detailed above, were isolated.

The former group of tubers is the only one of the six in which a majority, 53 per cent, of the tubers showed "no discoloration." The nearest approach to this is in the group which gave "miscellaneous fungi," of which, however, only 16 per cent had "no discoloration." A little over one-fourth, 28.7 per cent, of the tubers which gave "no organism" were lightly discolored, "yellowed," and about one-sixth, 16.5 per cent, were "browned." A very small percentage were affected by "end rot" or were "blackened," 1 and 0.8 per cent, respectively.

To sum up a portion of the data in Table I, it seems clearly indicated that the presence of a discoloration in the stem-end vascular region of a potato tuber is usually though not always evidence of the presence of an organism there. Even distinct discoloration, though, does not always mean the presence of an objectionable organism, for only about 45 per cent of the tubers distinctly discolored contained wilt or other disease-producing organisms, while the other 55 per cent yielded either miscellaneous fungi of no apparent consequence or no organisms whatever. In this connection it is to be borne in mind that the cultures made are of course not a perfect index to the organisms present, as is mentioned more in detail in a later paragraph. Neither does the absence of discoloration always indicate the absence of a serious organism, for about 5 per cent of all the tubers which were not discolored gave disease-producing organisms when cultured. A general conclusion that seems to be well justified is that the variation in the degree of discoloration caused by any one fungus in different tubers is so large and the differences in the type of discoloration caused by the various fungi are so small that the character of the discolorations can not be taken as a guide to what fungus is present or even as proof that any fungus is present.

OCCURRENCE OF MORE THAN ONE ORGANISM IN THE SAME POTATO TUBER

In any consideration of the occurrence of fungous organisms in the stem end of potato tubers the question naturally arises as to whether commonly more than one organism occurs at one time in the same tuber. In order to throw some light on this point a special set of cultures was made. One lot of 150 Up-to-Date tubers grown in 1917 in hills from plants badly wilted by *Verticillium albo-atrum* were cultured from all four quarters by the sweet clover stem method already described. In this case, after the tubers were treated and dried, the outer tissues at the stem end were cut away and the end was quartered by two longitudinal cuts at right angles to each other. A portion of the end of each of these quarters, including discolored vascular tissues whenever present, was then taken and placed in tubes of culture medium for incubation. The results, given in Table II, show that 64 tubers, or 42.6 per cent, gave *V. albo-atrum* in all four quarters, one tuber gave *Penicillium* sp. in the four quarters included in this case under "miscellaneous fungi,"

and four tubers gave no organisms in any of the four quarters. This makes 69 tubers, or 46 per cent of the lot, which gave identical results from the four quarters of each tuber. Forty-six others, or about 31 per cent, gave only one organism from a part of the quarters, varying from one to three, but not from all of the four quarters, the other quarter or quarters yielding no organism. There is thus a total of 77 per cent of the tubers which did not give more than one organism from each tuber. Thirty-four tubers, or about 23 per cent, gave two separate organisms, and one tuber gave three separate organisms from different quarters of the same tuber.

TABLE II.—*Organisms isolated from the stem end of the four longitudinal quarters of 150 Up-to-Date potato tubers harvested in 1917 from hills badly wilted with Verticillium albo-atrum*

Number of quarters yielding organisms.	Number of tubers with the four quarters of the inner vascular region at the stem end discolored as follows:													
	4 browned.	3 browned, 1 yellowed.	3 browned, 1 not discolored.	2 browned, 2 yellowed.	2 browned, 1 yellowed, 1 not discolored.	2 browned, 2 not discolored.	1 browned, 3 yellowed.	1 browned, 2 yellowed, 1 not discolored.	1 browned, 1 yellowed, 2 not discolored.	4 yellowed.	3 yellowed, 1 not discolored.	2 yellowed, 2 not discolored.	1 yellowed, 3 not discolored.	4 not discolored.	Total.
4 *V. albo-atrum*	34	5	6	2	6	2	1	1	1	5	1	....	....	....	64
3 *V. albo-atrum*, 1 miscellaneous fungi	5	3	1	....	....	....	1	1	....	2	....	....	....	....	13
3 *V. albo-atrum*, 1 none	7	2	12	3	2	....	....	1	....	2	....	....	....	....	29
2 *V. albo-atrum*, 1 *F. oxysporum*, 1 miscellaneous fungi	1	....	....	....	....	....	....	....	....	....	....	....	....	....	1
2 *V. albo-atrum*, 1 *F. oxysporum*, 1 none	....	1	....	....	....	....	....	....	....	....	....	....	....	....	1
2 *V. albo-atrum*, 2 miscellaneous fungi	3	....	....	1	....	....	....	....	....	....	....	....	....	....	4
2 *V. albo-atrum*, 1 miscellaneous fungi, 1 none	....	....	2	....	....	....	1	1	....	1	1	....	1	3	10
2 *V. albo-atrum*, 2 none	1	....	1	....	....	1	....	....	....	....	2	....	....	1	6
1 *V. albo-atrum*, 3 *F. oxysporum*	1	....	....	....	....	....	....	....	....	....	....	....	....	....	1
1 *V. albo-atrum*, 2 *F. oxysporum*, 1 none	....	1	....	....	....	....	....	....	....	....	....	....	....	....	1
1 *V. albo-atrum*, 1 *F. oxysporum*, 2 none	....	....	....	....	....	....	....	....	....	....	....	....	1	....	1
1 *V. albo-atrum*, 1 *F. radicicola*, 2 none	....	....	....	....	....	....	....	....	....	....	....	....	....	1	1
1 *V. albo-atrum*, 3 miscellaneous fungi	....	1	....	....	....	....	....	....	....	....	....	....	....	....	1
1 *V. albo-atrum*, 2 miscellaneous fungi, 1 none	....	....	....	....	....	....	....	....	....	....	1	....	....	....	1
1 *V. albo-atrum*, 3 none	....	....	1	1	....	....	....	....	....	....	....	1	1	....	4
4 miscellaneous fungi	1	....	....	....	....	....	....	....	....	....	....	....	....	....	1
3 miscellaneous fungi, 1 none	1	....	....	....	....	....	1	....	....	....	....	....	....	....	2
2 miscellaneous fungi, 2 none	....	....	1	....	....	....	....	....	....	1	....	....	....	1	3
1 miscellaneous fungi, 3 none	....	....	....	....	....	....	....	....	....	....	....	....	....	2	2
4 none	....	....	....	....	....	....	....	....	....	....	....	....	....	4	4
Totals	54	13	24	7	8	3	4	4	1	11	5	1	3	12	150

Table II shows five tubers from which both *Verticillium albo-atrum* and *Fusarium oxysporum* were isolated in cultures from different quarters. The cultures from one of these tubers are shown in Plate 141, B. This offers a possible explanation of some otherwise confusing results secured during the course of this investigation. For instance, in a few cases *F. oxysporum* was isolated from seed potatoes which when planted in clean soil gave rise to plants that wilted from attacks of *V. albo-atrum*. In cases of this kind the latter fungus may also have been present in

the seed potato when planted and, being the more vigorous organism of the two in this locality, caused the death of the plant. The indication at least is that while the great majority of tubers give only one organism in culture there are not uncommonly also a number which give two or occasionally more organisms, even two wilt-producing organisms, from different portions.

In considering the data that have been presented in Tables I and II, the question arises as to the accuracy of the information derived from the isolation cultures where only one culture is made from each tuber. It is quite likely that a number of the tubers recorded in Table I from which no organism was secured had, as a matter of fact, been invaded by some organism. This would seem to be particularly true of those affected by endrot. Yet in general the results seem to be in accord with probability. For instance, a very much larger percentage of all of the "not discolored" tubers than of those that were "yellowed" or "browned" gave no organism, the percentages being 81.6, 50.5, and 21.9, respectively. It has already been noted that of the lot of tubers referred to in Table II from each of which four cultures were made, 69 tubers, or 46 per cent, gave identical results from the four quarters of each tuber. Forty-eight others, or about 32 per cent, gave identical organisms in three of the quarters of each tuber; and 26 tubers, or about 17 per cent, in two of the quarters of each tuber. From the standpoint of chance, one single culture made from each of these 143 tubers would have given an accurate index to the organisms present in a total of 118 tubers, or 82.5 per cent of the group. A single culture made from each of the remainder would not necessarily have represented the exact conditions, although even here it would have shown the real situation more often than not, for in many cases the fungi secured came from the quarter or quarters having the most discoloration, and where only one culture was made it was always made from the most heavily discolored portion. From these data it is believed that the method for making the cultures in this investigation, though offering some chance of failure in securing correct evidence as to the organisms present, is still at least reliable enough to give a very good indication of the facts. It has seemed also to be the most practical method available where a large number of cultures had of necessity to be made in a comparatively short time and where it was desired, as in this case, to keep the tubers in as nearly natural condition as possible for purposes of planting for further records.

RELATION BETWEEN SIZE OF POTATO TUBERS AND OCCURRENCE OF ORGANISMS THEREIN

The question arises as to whether tubers of a certain general size are more likely to be free from internal infection than others and might, therefore, be selected out for planting with the expectation of getting a smaller amount of disease from them than from tubers of other sizes. There is

no theoretical reason for supposing that there would be any correlation between size and percentage of infection except that tubers from diseased plants are likely to be smaller than those from healthy plants, although late-formed tubers which would tend to be small in size would also be likely to show less infection than older ones because exposed to danger of invasion by the fungus for a briefer period. This would perhaps be counterbalanced by the presence of a larger amount of infective material in a field at the close of the season than at the start, due to the general progress of the disease.

To secure evidence bearing on this subject a tabulation was made of the data in hand, which includes results from 12,136 tubers. This is given in Table III and is partly shown in figures 3 and 4. These are the same tubers from which Table I was made, and they were grown under a variety of conditions, during three seasons from nine varieties, some by diseased

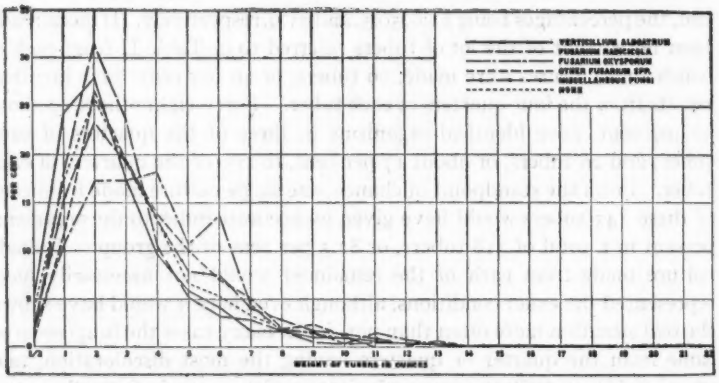

FIG. 3.—Diagram prepared from the horizontal percentages given in Table III, showing the percentage occurrence of a given organism in tubers of different weights.

and others by healthy plants. The results show that in general the organisms dealt with do not seem to occur considerably more in one size of potato tuber as measured by weight than in another, though there are a few noticeable differences. For instance, in figure 4, which shows the percentage occurrence of different organisms in tubers of a given weight, it will be seen that *Verticillium albo-atrum* was present to a smaller extent in the medium-sized tubers than in those of small or of large size, there being a steady decrease in percentage of this organism from 25.5 in the tubers weighing ½ ounce down to 9 in those weighing 7 ounces, then an increase up to 16.4 per cent in the 11-ounce tubers. And when comparisons are made between organisms from the standpoint of percentage of a given organism in tubers of different weights (fig. 3) then it will be seen that a greater proportion of all the tubers giving *V. albo-atrum* in

culture were small than was true in the case of any other organism. This relation may be further indicated by a specific comparison with the tubers which gave no organism when cultured. In the tubers weighing less than 3 ounces the percentage of all the tubers giving *V. albo-atrum* is higher than that of those giving no organism, while at 3 ounces and above the relative position of the two lots is reversed.

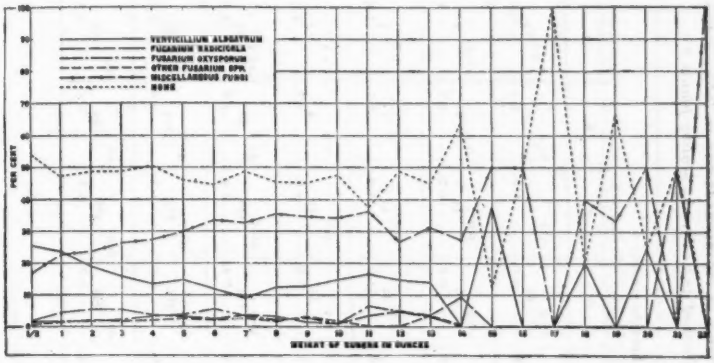

FIG. 4.—Diagram prepared from the vertical percentages given in Table III, showing the percentage occurrence of different organisms in tubers of a given weight.

Fusarium radicicola (fig. 3) occurred relatively more in the 2-, 3-, and 4-ounce tubers and less in the smaller and the larger tubers than did *Verticillium albo-atrum*. *F. oxysporum* occurred to a less extent than the other organisms in the tubers weighing 3 ounces and under and more than the other organisms in those weighing from 4 to 7 ounces. There was a gradual increase in percentage of "miscellaneous fungi" (fig. 4) from 16.6 in the ½-ounce up to 36.1 in the 11-ounce tubers. In the same range of tuber weights there was a fairly uniform decrease in percentage of "no organisms" isolated from 54.1 down to 37.7. Above 13 ounces there were so few tubers available for tabulation that the results for all the organisms isolated are variable.

The two chief lessons to be gained from these data are (1) that the smaller potatoes should not be used for seed purposes, because they are apt to contain a higher percentage of wilt infection than the medium-sized tubers unless it is known that the plants by which they were grown were free from wilt, in which case, of course, the small potatoes could be used with safety, and (2) that wilt can not be avoided merely by the selection from the bin of only the medium-sized or even the larger healthy-looking potatoes, as even these may contain a high percentage of wilt infection.

TABLE III.—*Relation between size of potato tubers, as measured by weight, and occurrence of organisms therein in tubers grown during the seasons of 1915, 1916, and 1917, under various conditions, some by diseased and others by healthy plants* [a]

Organisms isolated.	Tubers weighing (in ounces)—											
	½	1	2	3	4	5	6	7	8	9	10	11
Verticillium albo-atrum	25.5 108 5.1	23.4 506 24.1	18.9 585 27.9	15.8 366 17.5	13.2 201 9.6	14.6 122 5.8	11.9 83 4.0	9.0 35 1.6	12.4 31 1.5	12.7 19 0.9	14.7 16 0.8	16.4 10 0.5
Fusarium radicicola	1.9 8 1.6	4.3 93 18.0	5.2 162 31.4	5.3 123 23.8	3.6 55 10.6	3.1 26 5.0	2.3 16 3.1	3.6 14 2.7	3.2 8 1.6	1.3 2 .4	.9 1 .2	3.3 2 .4
Fusarium oxysporum	1.4 6 2.0	1.5 32 10.8	1.6 51 17.3	2.2 51 17.3	3.5 53 18.0	3.8 32 10.8	5.7 40 13.6	3.4 13 4.4	2.0 5 1.7	2.7 4 1.4	.9 1 .3	6.5 4 1.4
Other Fusarium species	.5 2 .9	1.2 26 11.9	1.9 58 26.5	1.8 43 19.6	2.0 30 13.7	2.6 22 10.0	2.2 15 6.9	2.8 11 5.0	1.6 4 1.8	3.3 5 2.3	1.8 2 .9	
Miscellaneous fungi	16.6 70 2.2	22.5 485 15.4	23.6 730 23.2	26.1 605 19.2	27.3 417 13.2	29.9 250 7.9	33.3 233 7.4	32.5 126 4.0	35.2 88 2.8	34.7 52 1.6	34.0 37 1.2	36.1 22 .7
None	54.1 229 3.9	47.1 1,019 17.4	48.8 1,511 25.8	48.8 1,132 19.3	50.4 769 13.1	46.0 384 6.6	44.6 312 5.3	48.7 189 3.2	45.6 114 2.0	45.3 68 1.2	47.7 52 .9	37.7 23 .4
Totals	100 423 3.5	100 2,161 17.8	100 3,097 25.5	100 2,329 19.1	100 1,525 12.6	100 836 6.9	100 699 5.8	100 388 3.2	100 250 2.1	100 150 1.2	100 109 .9	100 61 .5

Organisms isolated.	Tubers weighing (in ounces)—										Total.
	12	13	14	15	16	17	18	19	20	21	22	
Verticillium albo-atrum	14.6 6 0.3	13.8 4 0.2		37.5 3 0.1			20.0 1 0.05		25.0 1 0.05			17.3 2,097 100
Fusarium radicicola	4.9 2 .4	3.4 1 .2	9.1 1 .2				20.0 1 .2			50.0 1 .2		4.2 516 100
Fusarium oxysporum	4.9 2 .7	3.4 1 .3										2.4 295 100
Other Fusarium species		3.4 1 .5										1.8 219 100
Miscellaneous fungi	26.8 11 .3	31.1 9 .3	27.3 3 .1	50.0 4 .1	50.0 5 .2		40.0 2 .1	33.3 1 .03	50.0 2 .1		100 1 .03	26.0 3,153 100
None	48.8 20 .3	44.9 13 .2	63.6 7 .1	12.5 1 .01	50.0 5 .1	100 3 .1	20.0 1 .01	66.7 2 .03	25.0 1 .01	50.0 1 .01		48.3 5,856 100
Totals	100 41 .3	100 29 .2	100 11 .1	100 8 .1	100 10 .1	100 3 .02	100 5 .04	100 3 .02	100 4 .03	100 2 .02	100 1 .01	100 12,136 100

[a] In each box the middle set of figures shows the number of tubers which in culture gave the results indicated in the headings of the intersecting columns; the lower right set of figures gives the percentage this number is of the total tubers represented in the horizontal column; and the upper left set gives the percentage of the total tubers in the vertical column.

RELATION BETWEEN ORGANISMS IN SEED POTATOES AND ORGANISMS IN YIELDS

The extent to which organisms present in the seed potatoes were transmitted to the yields as indicated by cultures from the 1917 crop appears in Table IV. Plants grown from seed potatoes from which *Verticillium albo-atrum* was isolated before planting frequently developed wilt (Pl. 140, A) and gave 29.7 per cent of Verticillium infection in the yields. However, not all of the plants grown from the known Verticillium-infected seed were affected by the wilt disease, consequently the percentage of diseased tubers in the yields was considerably lower than it would have been if all the plants had wilted. It was high enough, however, to indicate that infected seed is a very serious factor in carrying the disease from one year to the next. The tubers produced by one lot of rather badly wilted plants showed 40.2 per cent infection with *V. albo-atrum* when cultured, and another lot gave a crop containing 49 per cent infection. The highest percentage of Verticillium infection found in the tubers produced by any considerable number of plants was 92. This result was secured in the yield of 28 plants of the variety Up-to-Date, which is very susceptible to this wilt. In a number of instances individual plants of several different varieties have given yields with 100 per cent Verticillium infection. The average, however, as shown by the records, is nearer 30 to 50 per cent. Some of the plants grown on clean soil from tubers from which either other organisms than *V. albo-atrum* or no organisms were isolated before planting also gave a rather large percentage of Verticillium infection in the yields. For instance, the seed potatoes from which only "miscellaneous fungi" were isolated gave 13.3 per cent Verticillium infection in the yields, and those from which no organisms were isolated gave 18.9 per cent Verticillium infection. This high wilt infection in these two lots apparently came from the spread of the Verticillium fungus from neighboring diseased plants in the field during the growing season, as will be shown more in detail in a later paper.

Fusarium radicicola occurred in only slightly larger amounts in the yields produced from seed potatoes that contained this fungus than it did in those from seed potatoes which according to the cultures made were free from it when planted. For instance, the seed tubers from which *F. radicicola* had been isolated gave back 9 per cent *F. radicicola* infection in the yields, while those from which *F. oxysporum* alone had been isolated gave 8.6 per cent *F. radicicola* infection in the yields, and those from which *Verticillum albo-atrum* alone had been isolated gave 4.4 per cent *F. radicicola*. Practically every lot of tubers cultured during this study has given a noticeable percentage of infection from *F. radicicola* regardless of whether this fungus was proved to be present in the seed potatoes or not. Thus, the indications are that it is transmitted to a slight extent in seed potatoes, that it may come from the soil and is evidently rather commonly distributed. This latter conclusion is in harmony with the work of Pratt (11), who secured this fungus in culture several times from Idaho soils never cropped with potatoes.

TABLE IV.—*Transmission of organisms from seed potatoes to yields in six varieties, season of 1917*[a]

Organisms isolated from seed potatoes.	Number of hills.	Tubers in yield from which were isolated—						Totals.
		Verticillium albo-atrum.	*Fusarium radicicola.*	*Fusarium oxysporum.*	Other Fusarium species.	Miscellaneous fungi.	No organism.	
Verticillium albo-atrum.	151	325 29.7	48 4.4	17 1.6	28 2.6	360 32.9	316 28.9	1,094 100
Fusarium radicicola.	21	3 2.1	13 9.0	5 3.5	2 1.4	67 46.5	54 37.5	144 100
Fusarium oxysporum.	146	101 9.7	89 8.6	39 3.8	19 1.8	346 33.2	447 42.9	1,041 100
Other Fusarium species.	16	8 7.0	3 2.6		5 4.3	20 17.4	79 68.7	115 100
Miscellaneous fungi.	143	131 13.3	39 3.9	4 .4	27 2.7	293 29.7	493 50.0	987 100
None.....	151	204 18.9	42 3.9	17 1.6	31 2.9	317 29.4	466 43.3	1,077 100
Totals.....	628	772 17.3	234 5.3	82 1.8	112 2.5	1,403 31.5	1,855 41.6	4,458 100

[a] In each box the upper set of figures shows the number of tubers which in culture gave the results indicated in the headings of the intersecting columns; and the lower right set of figures gives the percentage this number is of the total tubers represented in the horizontal column.

Similarly *Fusarium oxysporum* occurred somewhat more abundantly in yields grown from known *F. oxysporum* infected tubers than it did in those grown from tubers not known to be infected with this fungus, though in some cases the differences were very slight. For instance, 3.8 per cent *F. oxysporum* infected tubers came from seed known to be infected with *F. oxysporum*, whereas 3.5 per cent, almost as much, came from seed tubers which cultures had indicated to be infected only with *F. radiciola* when planted. It is true with *F. oxysporum* also that in practically every lot of potatoes cultured it was secured from at least a few tubers, even though it was apparently not present in the seed potatoes, indicating that it came from the soil and may be rather commonly distributed. This is in agreement with the findings of other workers (*1*, *6*). The small amount of wilt (Pl. 140, B) caused by this fungus in western Oregon and the low transmission from the seed potatoes to the yields, which was rather unexpected, is thought to indicate that this disease is

not highly virulent in this region. It may, however, be due in part to the apparent general tendency of *F. oxysporum* in the seed potatoes to fail to perpetuate itself in the plants grown therefrom, as shown by the work of Bisby (*1*) and MacMillan (*6*).

Occasionally potato tubers having the stem end sunken and discolored gave both *Fusarium oxysporum* and a small mite in culture. In a few cases both of these organisms were evidently transmitted from the seed potatoes to the yields. For instance, in one hill (Pl. 141, A) grown from a seed tuber from which these two forms were isolated before planting, three out of the nine tubers produced gave the same organisms in culture after harvest. The presence of the mite was no doubt responsible for the sunken condition of the stem end of the invaded tubers, as it naturally would consume some of the tissues and the skin would collapse; and, generally, tubers containing *F. oxysporum* alone appeared quite if not entirely normal on the exterior.

There was a slight tendency of the "other Fusarium species" to be transmitted to the yields, as these organisms ran highest in the tubers grown from similarly infected tubers. Some of these organisms also were found to occur more or less indiscriminately in any lot of tubers cultured.

There was no indication that any of the "miscellaneous fungi" were transmitted to an appreciable extent. They seemed to occur promiscuously with no apparent relation to the condition of the seed potato at planting time.

The seed potatoes from which "no organisms" were isolated gave crops which frequently showed the presence of organisms, doubtless derived from the soil or from adjacent diseased plants, although never to the extent of disease-infected seed.

In order to determine whether or not the stem-end seed piece would consistently transmit a higher percentage of organisms than the eye-end seed piece from the same tubers, a tabulation was made of the available data, the essential points of which are given in Table V. The kind of seed pieces used made no essential difference in the amount of infection from *Verticillium albo-atrum* secured either in the plants produced or in the yields obtained, the percentage of infection in the yields from the stem pieces being 22.7 and from the eyepieces 24.6. This difference is entirely negligible, being even less than the difference in the results secured from planting the two longitudinal halves of other tubers which presumably should have shown no difference in amounts of infection in the yields. However, in view of evidence later secured on the spread of *V. albo-atrum* from one plant to another in the row, the results presented here on the transmission of this organism in the different kinds of seed pieces must not be given too great weight, because the plants from the different kinds of seed pieces were grown in juxtaposition in the row, thus giving the fungus opportunity to spread from one plant to another.

Nevertheless, the results so far as they go are in agreement with the findings of Pethybridge (9) in Ireland, who has demonstrated that this wilt fungus is not localized at or near the stem end of affected tubers. There is, therefore, no particular value in the attempt to avoid Verticillium-wilt in seed potatoes by discarding the stem ends and planting only the eye ends of tubers suspected of containing this wilt fungus. Reliance for the control of this disease should rather be placed on other methods which have been demonstrated to be effective.

TABLE V.—*Transmission of organisms from different portions of the same seed tubers and from whole seed tubers to the tubers yielded by six varieties, season of 1917*

Origanism isolated from seed potato.	Number of seed pieces planted.	Percentage of same organisms in yields as was present in the seed potato according to kind of seed piece used.				
		Stem pieces.	Eye pieces.	One longitudinal half.	Other longitudinal half.	Whole tubers.
Verticillium albo-atrum	151	22.7	24.6	17.4	20.5	35
Fusarium radicicola	21	12.9	4.3	4.5	5.9	14.7
Fusarium oxysporum	146	2.9	2.3	7.7	5.8	3.8

Fusarium radicicola occurred noticeably more in the yields from the stem pieces than from the eyepieces, 12.9 per cent and 4.3 per cent, respectively. The number of seed pieces planted containing this fungus were so few that definite conclusions can not be drawn, and the differences noted might not hold true in an examination of a larger number of cases.

Fusarium oxysporum was transmitted to such a small extent in any of the potatoes experimented with that it is difficult to judge whether the stem-end pieces tend generally to give more disease than the eye-end pieces. A few tubers, though, apparently gave striking evidence of this tendency (Pl. 139, C). For instance, one infected tuber gave 75 per cent infection in the yield from the stem-piece plant and no infection in that from the eye-piece plant; another gave 33 and 14 per cent, and another gave 10 and 0 per cent, respectively. The average results, however, do not point strongly in this direction, and it is apparently true with this organism also that the practice of discarding the stem ends of seed potatoes is not a reliable method for the control of the disease and ought to be abandoned in favor of other more effective methods.

DISTRIBUTION AND IMPORTANCE OF VERTICILLIUM ALBO-ATRUM, FUSARIUM OXYSPORUM, AND FUSARIUM RADICICOLA IN OREGON

Although there has been no opportunity to make a systematic survey of these potato diseases in the entire State of Oregon, a number of scattered collections have been made in different regions and many specimens have been sent in by growers and by county agricultural agents. There remain sections, however, where potatoes are grown and

from which no specimens have been secured. The data presented here must, therefore, be considered incomplete. The status of these diseases is better known in western Oregon, the region west of the Cascade Mountains, than it is in the central and eastern portions.

Verticillium albo-atrum has been found in 16 counties, which embrace most of the important potato-growing areas of the State (fig. 5). It is widely distributed and of common occurrence at least in western Oregon, and every season causes an appreciable loss in many fields. The highest percentage of plants wilted from this fungus found in any commercial field was 30. The more usual amounts found are from 5 to 7 per cent. In the work on certification of potatoes in 1918, Verticillium-wilt was

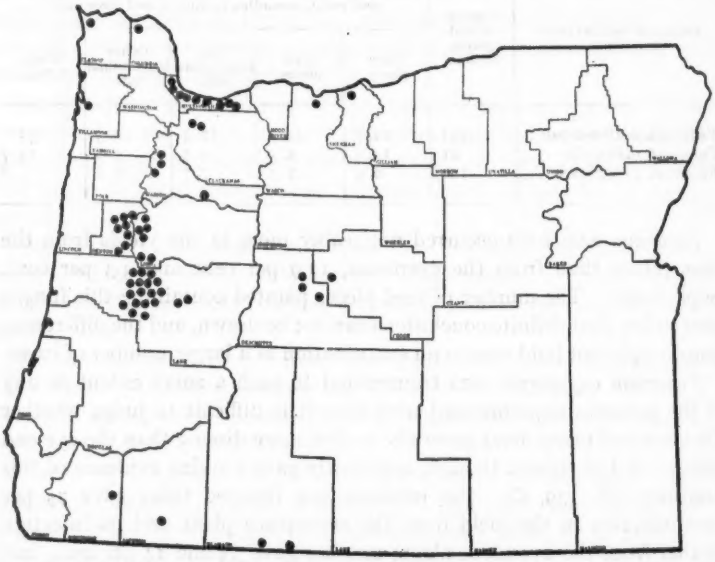

FIG. 5.—Map of Oregon, showing the localities where *Verticillium albo-atrum* has been collected on potatoes during the past few years.

the second factor in the order of importance in causing the failure of fields entered to pass the inspections. In this certification work or in any seed plot improvement work it is very necessary, therefore, to give due consideration to the nature of the disease and to the ways in which it is disseminated.

The yields of plants affected with Verticillium-wilt are usually greatly reduced, which may be indicated by a few specific examples.

Two plots of potatoes consisting of 73 hills each were grown in 1917 to test the influence of Verticillium-wilt on the yields produced. The seed tubers used were produced by apparently wilt-free plants and gave *Verticillium albo-atrum* in no case in cultures made before planting. They were each cut in two lengthwise, one half being planted in one plot

and the other half in the other plot, so that the seed employed was presumably quite disease-free and was as nearly identical in the two plots as possible. In one plot the seed pieces were inoculated by placing on top of each a culture of *V. ablo-atrum* growing on sweet clover stems before covering them with soil in the furrow, and the other plot was left uninoculated as a control. The plots were located a short distance apart on the same kind of soil on which the crops had been well rotated and which had not grown potatoes for at least five years. Ninety-nine per cent of the plants on the inoculated plot were affected by *V. albo-atrum* before the

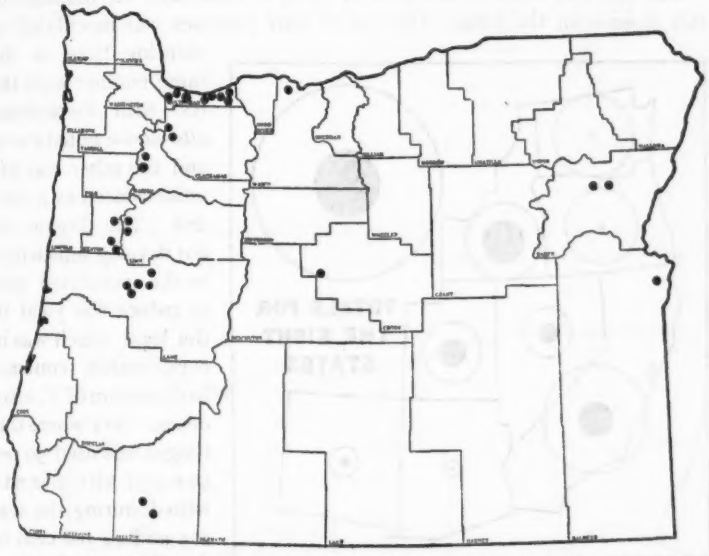

FIG. 6.—Map of Oregon, showing the localities where *Fusarium oxysporum* has been collected on potatoes during the past few years.

end of the season, and none of those on the control plot were found wilted. The yield on the diseased plot was 31 per cent less than that on the control plot.

In 1919 two ¼-acre plots were tested similarly. The seed used came from the same lot, but the tubers were not, as in the previous trial, cut longitudinally into halves and planted one in each plot. In this test there was a 59 per cent lower yield on the diseased than on the healthy plot. If the disease attacks the plants early in their growth the yield is usually greatly reduced, but if the attack comes late in the season the crop is practically normal in amount, though often a high percentage of the tubers carry the disease. The average reduction of yield in diseased plants probably ranges from 30 to 40 per cent.

Fusarium oxysporum has been found in 11 counties of Oregon in widely separated localities (fig. 6), though much less frequently then *Verticillium*

albo-atrum. In most cases it has been encountered attacking only scattering plants in the field and does not cause nearly so much damage as the other wilt organism. Only two fields—one in Lane County and the other in Multnomah County, both of western Oregon—have so far been reported to or seen by the writer where this fungus was recognized as causing a high percentage of disease. In the former field about 10 per cent and in the latter about 30 per cent of the plants were affected. The reason for these high percentages of infection in these two fields was not apparent.

One test was made at Corvallis in 1917, to determine the influence of this disease on the yield. One lot of seed potatoes was inoculated at planting time in the same manner as in the test with *Verticillium albo-atrum* noted above and the other was left uninoculated as a control. The disease did not develop sufficiently in the inoculated plot to reduce the yield in the least, which was in considerable contrast to the action of *V. albo-atrum*. For where this fungus was used 99 per cent of the plants wilted during the season and 49 per cent of the tubers were infected by the same fungus when cultured after harvest, but where *Fusarium oxysporum* was used less than 5 per cent of the plants showed wilt and only 6 per cent of the tubers were infected by this same fungus when harvested. According to all available information this disease must be considered of relatively minor importance in western Oregon. The data at hand do not justify any definite conclusions as to its importance in the eastern part of the State, where it may prove to be more serious.

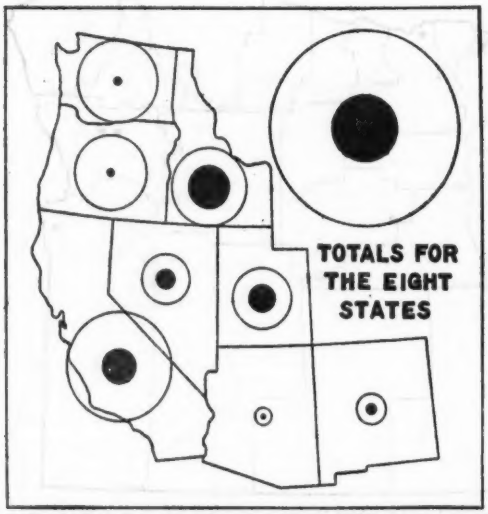

FIG. 7.—Map of eight western States, showing graphs of the production of potatoes in the different States in 1917 and the losses caused from wilt due to *Fusarium oxysporum*. The black area of the graph shows the loss from Fusarium-wilt; the white area, the production of potatoes; and the entire area, the production of potatoes if there had been no loss from Fusarium-wilt.

There are areas in the Pacific coast and mountain States where the Fusarium-wilt is without doubt a factor of considerable importance in potato growing. The Plant Disease Survey (*12*) has published estimates showing losses in these States in 1917, ranging from 1 to 30 per cent and

averaging 14 per cent (Table VI and fig. 7). The larger losses in this area occur in general in the hotter, irrigated sections. Oregon is included with an estimated loss of about 1 per cent.

TABLE VI.—*Effect of Fusarium-wilt on the yield of potatoes in the western United States in 1917 (12)*

State.	Production in 1917.	Estimated loss from Fusarium-wilt.	
	Bushels.	*Bushels.*	*Per cent.*
Washington	9,875,000	100,000	1
Oregon	8,100,000	82,000	1
California	15,225,000	1,691,000	10
Idaho	6,084,000	2,607,000	30
Nevada	3,105,000	548,000	15
Utah	4,347,000	1,087,000	20
Arizona	420,000	47,000	10
New Mexico	1,276,000	174,000	12
Total	48,432,000	6,336,000	[a] 14

[a] Average.

Fusarium radicicola has been secured from potatoes in nine counties of the State (fig. 8). It, too, is seemingly of common occurrence, but is

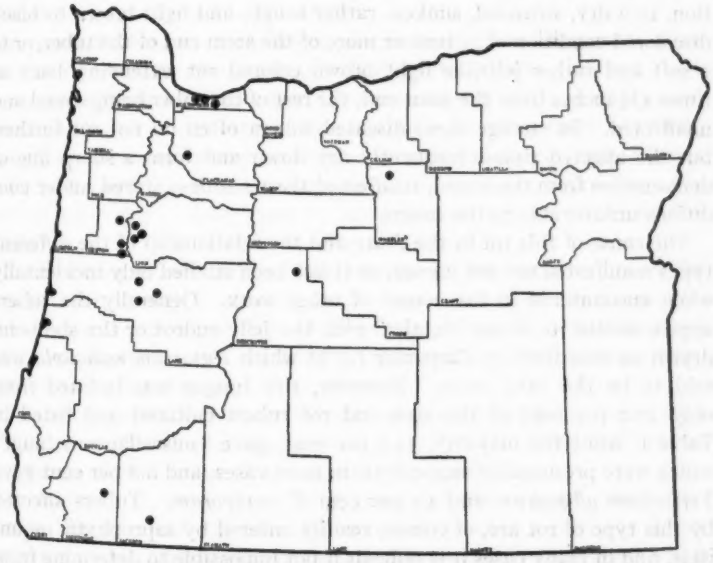

FIG. 8.—Map of Oregon, showing the localities where *Fusarium radicicola* has been collected on potatoes during the past few years.

apparently of little importance to potato production here. It has not been reported as a cause of wilt in other places and evidently does not often cause any wilt of the plants in Oregon, though the fact that it has

occasionally been isolated in pure cultures from discolored stem tissues of wilted plants suggests that it may occasionally cause a wilt of potato plants. It has been secured most frequently from tubers which were perfectly sound except for the presence of discoloration in the stem-end vascular region. For instance, 82.4 per cent of the tubers which gave this organism in cultures were browned or yellowed in this region (Table I) and were not in any way affected by rot. Only 8.3 per cent of the tubers which gave this fungus in culture were affected by stem-end rot of some form or other, varying from a dry, withered rot to a moist, soft, and light brown colored rot more typical of the condition known as "jelly end" rot. The specific black fieldrot of potato tubers due to *F. radicicola* as stated to occur in Idaho (*10*) and eastern Washington (*5*) has not yet been reported to or seen by the writer in Oregon. The conditions in the eastern part of the State remain largely, however, still to be investigated.

A stem-end rot of potato tubers occurs not infrequently during some seasons in western Oregon, and to some extent in the rest of the State, though in other seasons it is rarely encountered. It affects only the long tubers and varies widely in type and extent of rot at harvest time from a mere withering unaccompanied by discoloration of the stem end of the tuber as though a part of the water had been withdrawn from that portion, to a dry, wrinkled, sunken, rather tough, and light brown to black discolored condition of ½ inch or more of the stem end of the tuber, or to a soft and rather jellylike light brown colored rot extending back at times 1½ inches from the stem end, the rest of the tuber being sound and unaffected. In storage these diseased tubers often do not rot further, but the affected tissues frequently dry down and form a sharp line of demarcation from the sound, unaffected tissues unless stored under conditions unfavorable to the tubers.

The cause of this rot in the State and the relationship of the different types manifested are not known, as it has been studied only incidentally when encountered in the course of other work. Generally the tubers appear similar to if not identical with the jelly endrot or the stem-end dryrot as described by Carpenter (*2*) of which *Fusarium radicicola* was said to be the chief cause. However, this fungus was isolated from only 12.2 per cent of the stem-end rot tubers cultured and listed in Table I, while the majority, 53.9 per cent, gave "miscellaneous fungi" which were presumably saprophytic in most cases, and 8.8 per cent gave *Verticillum albo-atrum* and 4.5 per cent *F. oxysporum*. Tubers affected by this type of rot are, of course, readily entered by saprophytic organisms, and in many cases it is difficult if not impossible to determine from isolation cultures the primary cause of the trouble. However, the large variety of organisms secured in culture from affected tubers, the occurrence of the trouble only during certain seasons without any apparent relation to the condition of the seed potatoes at planting time or to crop rotation, and the presence of *F. radicicola* in the stem end of so many

tubers not affected by rot lead one to suspect that the appearance of the trouble depends more on climatic conditions than it does on the presence of any one of two or three organisms.

It seems possible and perhaps probable that when moisture in the soil is deficient in the latter part of the growing season, as it frequently is in western Oregon, and the transpiration of the plant is relatively excessive during hot weather the plant might, as sometimes occurs in fruits (*3*), actually withdraw water from the stem end of the tuber, giving a sunken withered condition favorable to the entrance of various organisms both parasitic and saprophytic. There might then be a gradual progress from this condition to typical jelly endrot, and in each case the condition of the tuber at harvest time would perhaps depend on the particular conditions surrounding it during growth and the period of maturing. It remains, however, for future work to determine what the facts in the case are. It should be stated that for the present no special measures for the control of this stem-end rot can be definitely recommended.

SUMMARY

The studies reported here were conducted in western Oregon, and the results apply to western Oregon conditions. They may not apply in their entirety to the rest of the State.

In western Oregon, *Verticillium albo-atrum* is more important than *Fusarium oxysporum* as a cause of wilt of potato plants. Each of these organisms is frequently present in the stem-end vascular region of potato tubers produced by diseased plants, and their presence there is usually though by no means always indicated by distinct discoloration of that region. An average of 6.6 per cent and occasionally as high as 14.4 per cent of the tubers which gave *V. albo-atrum* in culture were not discolored.

Fusarium radicicola also is often present in this same region of the potato tuber, though it is not known to be a cause of wilt of the plants; and the discoloration generally accompanying it cannot be distinguished from that usually present with the two common wilt-producing organisms, *Verticillium albo-atrum* and *F. oxysporum*.

Fusarium radicicola caused heavier discoloration than *Verticillium albo-atrum* in the infected tubers, while *F. oxysporum* caused still heavier discoloration than either of the other two organisms.

In addition to these three fungi there are also several others that invade the stem-end vascular region of potato tubers, and the longer the potatoes are kept in storage the larger is the number of tubers which give organisms in culture. Some of these are parasitic on potatoes and many others are not, so far as known, associated in any way with a disease of this crop. They are usually though not always accompanied by discoloration of the tuber tissues.

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The presence of discoloration in the stem-end vascular region of potato tubers is not a trustworthy index of the presence of disease-producing organisms therein and ought not to be relied upon exclusively as a guide for the separation of diseased from healthy tubers for planting purposes. For instance, 45 per cent of the tubers which were "browned" in the vascular region when cultured gave organisms which cause disease in potatoes, and 55 per cent gave either no organism or miscellaneous fungi of no apparent importance; 22 per cent and 5 per cent of those which were "yellowed" and "not discolored," respectively, gave organisms parasitic on potatoes, the others of these lots giving nothing of consequence.

Verticillium albo-atrum occurred in all sizes of potato tubers, though somewhat more extensively in the small ones than in those of medium size. *Fusarium oxysporum* and *F. radicicola* did not seem to occur considerably more in one size of potato tuber than in another. The medium-sized tubers gave a larger proportion of miscellaneous organisms than the smaller ones.

Verticillium albo-atrum is transmitted to a considerable extent from seed potatoes to yields. From 30 to 50 per cent of the tubers grown from known infected seed potatoes were invaded by the same organism when harvested and cultured. *Fusarium radicicola* and *F. oxysporum* were transmitted to only a slight extent from seed potatoes to yields and were apparently not infrequently present in soils which had not been planted to potatoes for several years.

The stem-end seed pieces did not seem to give more disease either in the plants or in the tubers produced therefrom than the eye-end seed pieces of the same infected tubers. The differences are at least so slight that it apparently is not advisable in attempting to avoid wilt in seed potatoes to rely much on the practice of discarding the stem ends and planting only the eye ends of tubers suspected of containing wilt organisms.

Verticillium albo-atrum is widely distributed in Oregon, having been recorded from 16 counties, and is the most important potato wilt-producing organism in the western part of the State. It causes appreciable losses each year, not only in commercial fields but especially in seed plots, because the presence of this fungus greatly lessens the value of the potatoes for seed purposes. It annually is responsible for the failure of a considerable number of fields to pass inspection for certification. The yields of affected plants are reduced on the average of from 30 to 50 per cent.

Fusarium oxysporum is also widely distributed in the State, having been noted in 11 counties, though it is seemingly of little importance, at least in the western portion. In only a few cases have any considerable number of plants been found attacked by this organism in any western Oregon fields examined.

Fusarium radicicola occurs frequently in potato tubers in Oregon, though it usually does not produce any apparent ill effects. It is often associated with a slight and generally rather dry, withered endrot or a soft and moist endrot, but it is not believed to be the sole cause of this trouble. It is more often found in tubers that are sound, except for having discolored vascular regions near the stem end.

A stem-end rot of potato tubers, varying from a mere withering of the stem end to a dry, withered, brown to black rot, or to a soft jellylike light brown rot, occurs rather commonly during some seasons in western Oregon. It appears to be due as much to climatic conditions during the growing season as to the presence of any certain parasitic organisms.

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PLATE 139

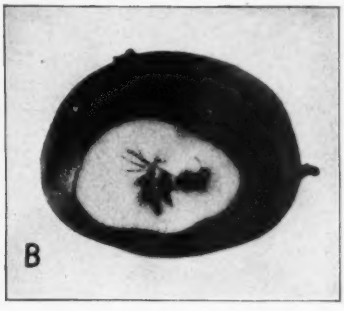
A.—Up-to-Date potato tuber with surface of stem end cut off to show discolored vascular tissue from which *Verticillium albo-atrum* was isolated in culture.

B.—Early Rose tuber from which *Fusarium oxysporum* was isolated.

On the average *F. oxysporum* caused heavier discoloration than did *V. albo-atrum* in the invaded tubers, though the appearance of the tubers could not be depended on for differentiating between the two organisms.

C.—Early Rose potato tuber from the discolored portion of which *F. oxysporum* was isolated in culture. The two plants grown from the two stem-end seed pieces became diseased, did not grow more than 9 inches in height, and died without producing any yield. The two plants from the two eye-end seed pieces remained healthy throughout the season and produced an average yield of 45 ounces. This difference in results from the stem-end and eye-end seed pieces is unusual, however, for on the average the former performed almost as well as the latter.

A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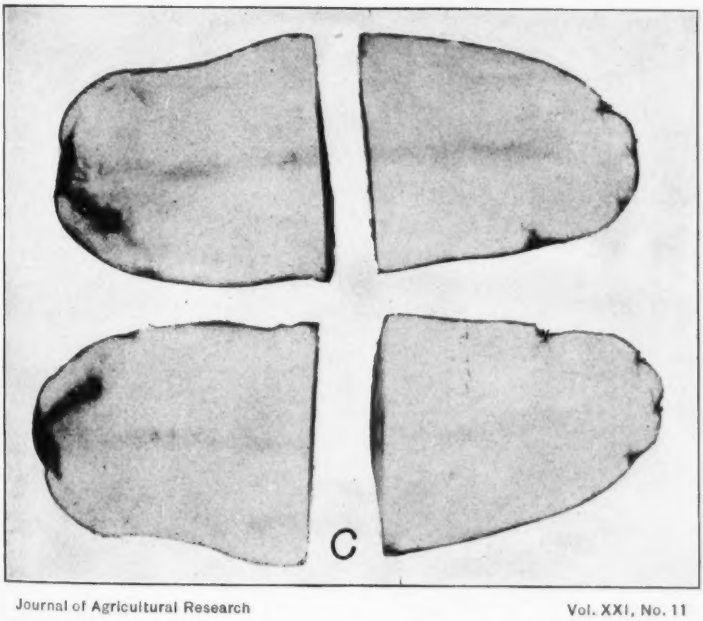
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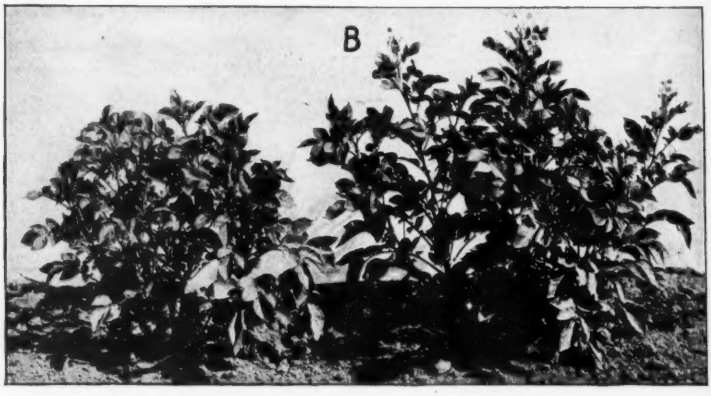
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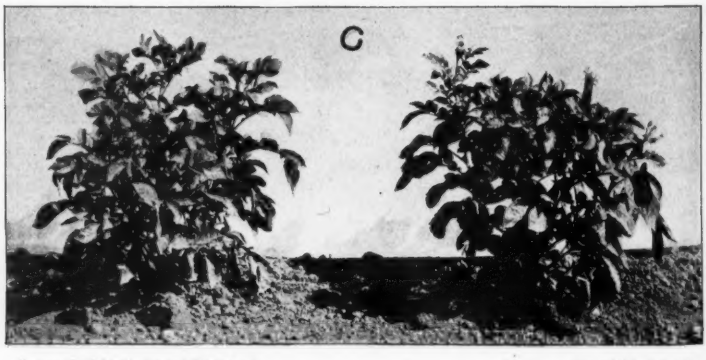
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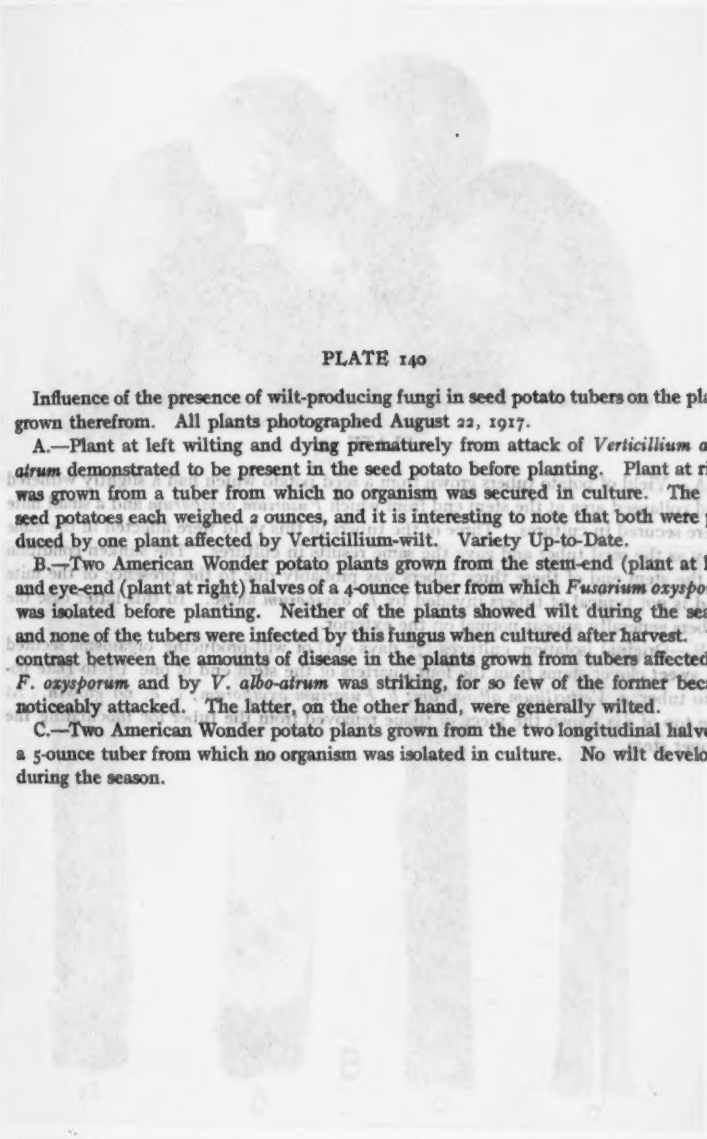


PLATE 140

Influence of the presence of wilt-producing fungi in seed potato tubers on the plants grown therefrom. All plants photographed August 22, 1917.

A.—Plant at left wilting and dying prematurely from attack of *Verticillium albo-atrum* demonstrated to be present in the seed potato before planting. Plant at right was grown from a tuber from which no organism was secured in culture. The two seed potatoes each weighed 2 ounces, and it is interesting to note that both were produced by one plant affected by Verticillium-wilt. Variety Up-to-Date.

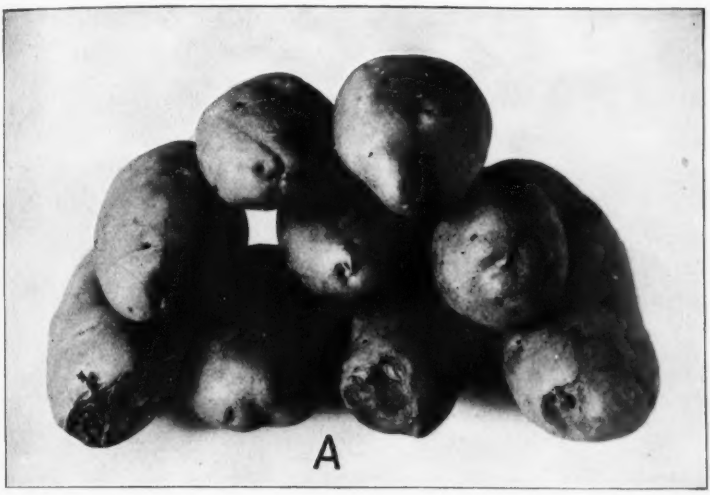
B.—Two American Wonder potato plants grown from the stem-end (plant at left) and eye-end (plant at right) halves of a 4-ounce tuber from which *Fusarium oxysporum* was isolated before planting. Neither of the plants showed wilt during the season and none of the tubers were infected by this fungus when cultured after harvest. The contrast between the amounts of disease in the plants grown from tubers affected by *F. oxysporum* and by *V. albo-atrum* was striking, for so few of the former became noticeably attacked. The latter, on the other hand, were generally wilted.

C.—Two American Wonder potato plants grown from the two longitudinal halves of a 5-ounce tuber from which no organism was isolated in culture. No wilt developed during the season.

PLATE 141

A.—Yield of potato tubers grown from a seed potato which had a slightly withered and collapsed area at the stem end from which *Fusarium oxysporum* and a small mite were secured in cultures. Three of the tubers in this yield were affected in the same way as the seed tuber and gave the same results in cultures. The sunken condition of the stem end of these three tubers was probably due to the presence of the mite and is not typical of tubers invaded by *F. oxysporum* alone. In this latter case the tubers generally appear normal on the exterior.

B.—Original isolation cultures (77 days old) of wilt-producing organisms secured on sweet clover stems from the four quarters of the stem end of one Up-to-Date potato tuber: *a*, *Verticillium albo-atrum*; *b*, *Fusarium oxysporum*; *c*, *d*, no growth. At the top of *d* is shown the piece of tissue removed from the tuber for inoculating the clover stem.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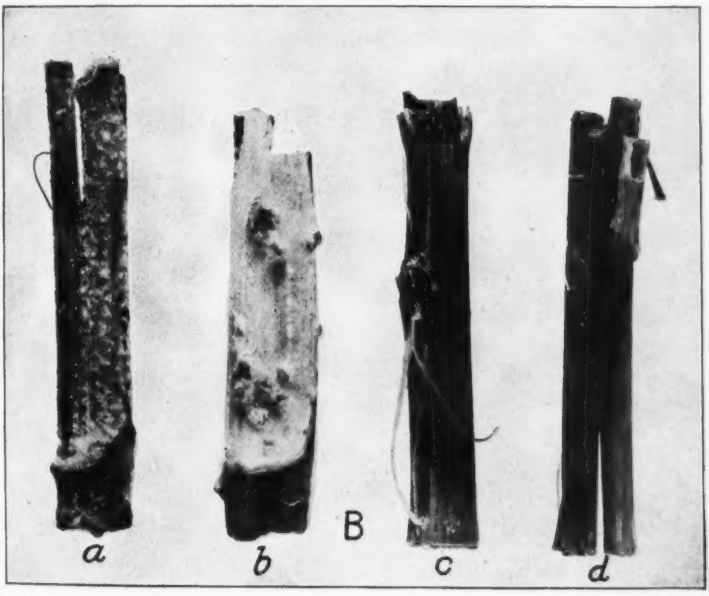
a
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B
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d

CORRELATION AND GROWTH IN THE BRANCHES OF YOUNG PEAR TREES [1]

By H. S. REED [2]
Professor of Plant Physiology, College of Agriculture, University of California

The present paper attempts to make a quantitative study of the relationships of laterals produced by the young branches of the pear tree. Such an inquiry should be of value both to the physiologist who is interested in the mechanism of development and to the horticulturist who is interested in the production of a tree of a given type.

In a previous paper (*10*)[3] it was shown that upright young pear shoots tend to remain unbranched so long as the apical bud grows uninterruptedly. If the apical bud is arrested in its development, or is removed, a neighboring lateral bud promptly develops and continues the lineal growth of that member. Moreover, if the apical portion of a shoot is amputated, the buds immediately below the point of amputation are not only the first to develop into shoots but produce the longest shoots.

A plantation of young Bartlett pear trees (*Pyrus communis* L.) growing at the Citrus Experiment Station, Riverside, Calif., furnished the data upon which this study is based. The trees were planted in the orchard in 1916, and the measurements were taken in February, 1920. The lateral shoots (Pl. 142), hereafter designated as "laterals," grew during the summer of 1919, and the mother shoots on which they were borne grew in the summer of 1918.

During the early life of the orchard, certain plots of the trees were systematically "headed back" to form a framework of a particular type. Accordingly these plots of trees were pruned in the winter of 1918–19 by amputating from one-half to three-fourths of all of the principal upright shoots grown in the preceding season. The portion remaining after pruning is designated as the "mother shoot" in the following discussion. The unpruned trees never received any pruning after the first year. The lateral shoots grew on the mother shoots during the summer of 1919. The relations of the two will be readily comprehended upon referring to Plate 142.

The mother shoots used in this study stood in an approximately vertical position and on the small trees were in no way crowded. The results are not, therefore, believed to be greatly influenced by differences

[1] Paper No. 78, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, Calif.

[2] The writer wishes to mention his indebtedness to Mr. F. F. Halma for assistance in the calculations and to Dr. J. A. Harris for valuable suggestions.

[3] Reference is made by number (italic) to "Literature cited," p. 874–875.

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in illumination. None of the trees had produced any fruit up to the time these measurements were made.

The two classes of mother shoots (pruned and unpruned) were on different trees. The 270 pruned mother shoots were on 91 trees which had received systematic "heading back"; the 54 unpruned mother shoots were on 25 trees which received no pruning. While this distribution does away with a certain closeness of spatial association, it prevents the possible transmission of influences from one class of mother shoots to the other.

In the present paper the term "growth" is used to designate a permanent increase in size. It is well recognized, however, that the same term may also be applied to phenomena in which there is little if any increase in size—for example, differentiation of organs and tissues.

The length of the lateral was taken as a simple measure of its growth. The almost complete absence of secondary laterals of any consequence allows this kind of measurement to be taken with a comparatively small error. Even where secondary laterals were produced there was no evidence that they had limited the length-growth of the primary lateral.

The shoots produced in a single season on a vigorous pear branch are usually of two kinds—"laterals" and "fruit spurs." The general characteristics of these two types of shoots have been discussed by Vöchting (*14*) and others. While it is convenient to consider the two types of shoots separately, it is necessary to remind the reader that their differences are primarily quantitative and not qualitative. The fruit spurs ordinarily attain but a short length and produce fruit-bearing buds. Under various circumstances they may, however, be forced to make strong vegetative growth and become "laterals." Such results often follow severe pruning or a change of position of the parent shoot whereby the dorsally placed "fruit spurs" will develop into vegetative "laterals" (*10*). A true dimorphism does not seem to exist in the young branches of the pear tree.

The "first" lateral is designated as the lateral at the distal end of the mother shoot, and the others follow in serial order toward the proximal end of the mother shoot. The "original" number of buds on a mother shoot was the number present before any laterals had grown—that is, at the beginning of the 1919 growing season.

The mother shoots on the pruned trees had a mean length of 44.1 cm. and a coefficient of variability of 39.2 per cent. The original number of buds on these mother shoots had a mean of 15.5 buds with a coefficient of variability of 41.1, and so elsewhere. The mother shoots on the unpruned trees had a mean length of 50.6 cm. with a coefficient of variability of 29. The number of original buds they possessed was 21.5 with a coefficient of variability of 25.2. The frequency distributions of these variants are shown in figure 1. Both distributions are asymmetrical and have a skewness in the direction of the higher values.

I. GROWTH AND DIFFERENTIATION OF LATERALS

The characteristic growth of laterals and fruit spurs on the mother shoots is to be regarded as an expression of their capacity to develop under the influence of the various internal and external factors at work. An analysis of their nature and variability ought to throw some light upon the laws of growth.

Such an analysis will involve an investigation of at least two phases of the laws of growth—first, the total quantity of shoot wood produced upon the mother shoots, and secondly, the differentiation found in the laterals produced upon the mother shoot. At all stages of the inquiry

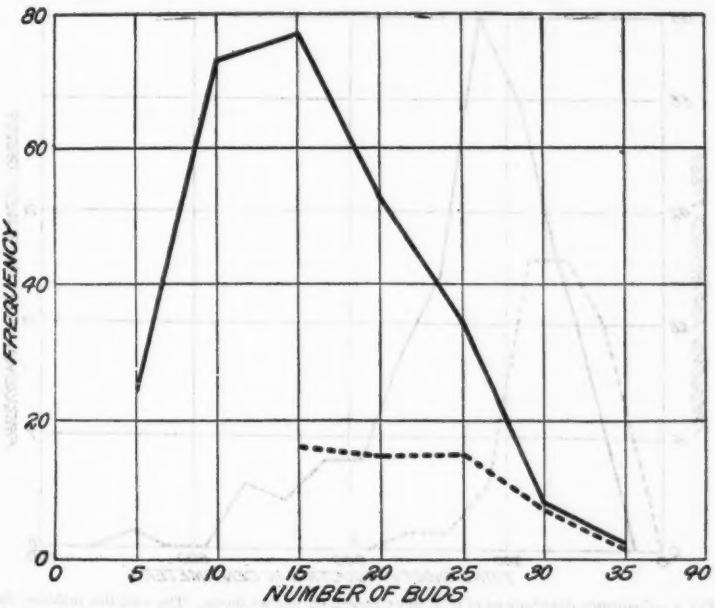

FIG 1.—Frequency distributions of buds on mother shoots. The solid line indicates distribution on pruned shoots and the broken line distribution on unpruned shoots.

it will be profitable to compare the growth produced on the pruned mother shoots with that produced upon mother shoots of similar age which received no pruning.

It will doubtless seem to some readers that the investigation treats the mother shoots to too great a degree as independent organisms. The only reply to such a criticism is that it seemed impossible to treat them in any other way. While correlative influences undoubtedly exist between the different mother shoots, it seems at present impossible to evaluate them. By using a sufficiently large population, it is probable that such correlated influences are to a large extent equalized. It may be stated, however, that the upright shoots on young pear trees are sufficiently uniform for all purposes of the present investigation.

TOTAL PRODUCTION OF LATERALS ON THE MOTHER SHOOTS

Reference to Tables I and II gives a general idea of the total length of all laterals produced upon the 324 mother shoots measured.[1] It is at once evident that there is pronounced variability in the total amount of new wood produced by individual mother shoots. The mother shoots which had been pruned in the preceding winter produced an average total growth of 251.5 ± 4.9 cm. The total shoot production of the pruned mother shoots ranged from 85 cm. to 685 cm., with an interquartile range of 148.53 cm. and a coefficient of variability of 44.91 per cent. The unpruned mother shoots produced an average total growth

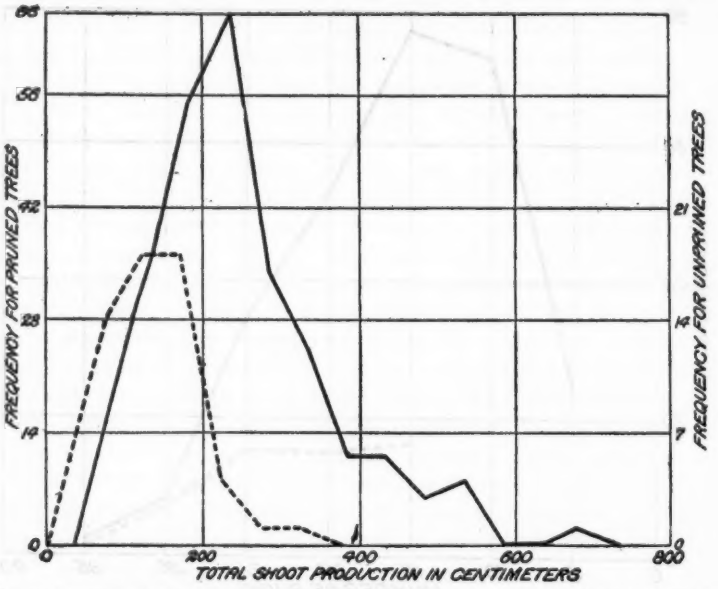

FIG. 2.—Frequency distributions of total shoot growth on mother shoots. The solid line indicates distribution on pruned shoots and the broken line distribution on unpruned shoots.

of 140.5 ± 5.3 cm. The total length of new shoots on unpruned mother shoots ranged from 75 cm. to 325 cm., with an interquartile range of 71.44 cm. and a coefficient of variability of 37.82 per cent. So far as these figures go, there is, therefore, slightly more variability in the total amount of new wood produced by the pruned mother shoots. The graphs in figure 2 show the nature of the two populations when the quantity of new wood produced is used as abscissa and the frequency as ordinate. The class range for the growth on the pruned shoots was 60 cm. and that for the growth on the unpruned shoots was 50 cm.

[1] The presentation of the actual measurements of the laterals would fill several very large tables. While I realize that these measurements should be published, it seems best in the interests of economy to summarize the data and give them in Tables I and II. The complete data are on file at the Citrus Experiment Station, and copies will be sent to workers who feel that they might profit by them.

TABLE I.—*Mean length of laterals on pruned mother shoots*

Lateral No.	On mother shoots which, after pruning, had—								
	4 to 6 buds.	7 to 9 buds.	10 to 12 buds.	13 to 15 buds.	16 to 18 buds.	19 to 21 buds.	22 to 24 buds.	25 to 27 buds.	28 to 37 buds.
	Cm.	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*	*Cm.*
I	126.6	121.2	114.5	110.2	110.5	103.6	101.4	97.7	97.2
II	73.6	71.4	69.6	68.3	60.2	70.9	72.1	76.6	73.3
III	38.7	42.2	31.8	33.5	29.2	22.1	29.3	31.1	16.5
IV	6.6	13.6	9.7	14.2	13.1	9.9	9.3	10.4	.3
V	.8	17.5	6.7	6.9	6.2	10.1	8.4	15.7	13.4
VI	0	1.7	.5	2.1	1.9	1.0	3.8	3.7	3.5
VII	.....	1.7	3.8	1.3	4.6	1.5	6.1	5.1	2.4
VIII	.....	.03	2.6	2.8	3.1	1.7	.7	3.3	.3
IX	.....	0	.2	.2	1.8	2.8	.3	1.2	1.1
X	.....	.....	.8	2.3	.5	1.3	1.7	.1	2.5
XI	.....	.....	.5	1.9	2.0	2.2	3.7	6.0	1.9
XII	.....	.....	0	.7	1.2	2.0	.4	.9	11.5
XIII	.....	.....	.....	1.5	.9	2.7	.8	3.1	.9
XIV	.....	.....	.....	0	.8	.3	.7	8.1	.8
XV	.....	.....	.....	0	.2	1.3	.3	1.1	2.3
XVI	.....	.....	.....	.....	1.6	1.1	.3	7.1	1.9
XVII	.....	.....	.....	.....	0	1.3	1.4	8.4	11.8
XVIII	.....	.....	.....	.....	0	.1	1.6	3.7	3.1
XIX	.....	.....	.....	.....	.....	1.3	3.4	2.2	7.6
XX	.....	.....	.....	.....	.....	0	.2	.4	.9
XXI	.....	.....	.....	.....	.....	0	.2	2.5	2.0
XXII	.....	.....	.....	.....	.....	.....	0	1.6	9.5
XXIII	.....	.....	.....	.....	.....	.....	0	9.9	.4
XXIV	.....	.....	.....	.....	.....	.....	0	9.7	7.4
XXV	.....	.....	.....	.....	.....	.....	.....	.2	6.6
XXVI	.....	.....	.....	.....	.....	.....	.....	3.3	.4
XXVII	.....	.....	.....	.....	.....	.....	.....	0	2.1
XXVIII	.....	.....	.....	.....	.....	.....	.....	.....	0
XXIX	.....	.....	.....	.....	.....	.....	.....	.....	0
XXX	.....	.....	.....	.....	.....	.....	.....	.....	0
XXXI	.....	.....	.....	.....	.....	.....	.....	.....	0
XXXII	.....	.....	.....	.....	.....	.....	.....	.....	0
XXXIII	.....	.....	.....	.....	.....	.....	.....	.....	0
XXXIV	.....	.....	.....	.....	.....	.....	.....	.....	0
XXXV	.....	.....	.....	.....	.....	.....	.....	.....	0
XXXVI	.....	.....	.....	.....	.....	.....	.....	.....	0
XXXVII	.....	.....	.....	.....	.....	.....	.....	.....	0
Total	246.3	269.3	240.7	245.9	237.8	237.2	246.1	313.1	281.6

These graphs give further evidence on the nature of the growth of new shoots on the pear tree.

In case the total amount of growth produced on the mother shoots were dependent upon mere accidents of position or other factors of pure chance, we should expect to find that its frequency distribution would approximate the normal curve of errors.

In both cases the frequency distributions depart rather widely from that of the normal curve of errors. The values for the growth on the pruned shoots were found to belong to Pearson's type IV curve of frequency distribution in Rhind (*12*), and those of the unpruned shoots to a type I curve. Both distributions are distinctly skew toward the higher values

and indicate that there is a tendency in the population as a whole to produce more than the mean quantity of wood. This tendency in the growth response may, however, be opposed by some factor in the tree which operates to cut down the number of individuals attaining greater length.

TABLE II.—*Mean length of laterals on unpruned mother shoots*

Lateral No.	On mother shoots which had—		
	12 to 19 buds.	20 to 27 buds.	28 to 36 buds.
	Cm.	*Cm.*	*Cm.*
Apical	70.3	66.1	66.3
I	18.8	9.1	28.0
II	18.7	20.3	27.3
III	6.9	4.9	6.9
IV	4.5	4.4	1.1
V	4.0	2.8	3.4
VI	3.0	1.4	1.3
VII	1.8	2.7	1.0
VIII	1.9	.9	4.0
IX	3.9	1.3	1.3
X	3.7	2.5	1.4
XI	1.8	2.7	1.7
XII	1.4	1.5	7.3
XIII	.7	3.4	1.4
XIV	.6	1.8	3.7
XV	.6	1.5	1.6
XVI	0	.8	1.9
XVII	0	2.0	1.3
XVIII	0	1.6	2.4
XIX	0	.7	2.9
XX	.....	.5	1.4
XXI	.....	.3	.7
XXII	.....	.4	.7
XXIII	.....	.2	1.4
XXIV	.....	.2	1.0
XXV	.....	.1	.4
XXVI	.....	.0	.4
XXVII	.....	.0	.3
XXVIII	.....	.....	0
XXIX	.....	.....	0
XXX	.....	.....	0
XXXI	.....	.....	0
XXXII	.....	.....	0
XXXIII	.....	.....	0
XXXIV	.....	.....	0
XXXV	.....	.....	0
XXXVI	.....	.....	0
Total	142.6	134.1	172.5

To attempt any far-reaching analysis of the causes of the greater range and variability in the shoot production on the pruned trees would be unprofitable with nothing more than the data at hand. There is evidence that the orientation of a shoot with respect to a perpendicular line has a controlling influence per se upon the amount and distribution of subsequent growth. In selecting the material for this study the at-

tempt was made, however, to avoid all shoots which to any measureable extent departed from the perpendicular. Further experimental work ought to be done to determine the ratio between the new material produced and the amount of shoot pruned off, as well as the ratio between the amount of new material produced and that left on the tree.

At this point the question may logically be asked, "Does the severity of the pruning affect the total amount of wood produced in the following season?" To answer the question we may consult the data given in Table III, which sets forth the mean total length of laterals produced on pruned and unpruned mother shoots. On the pruned trees the class range is three buds, on the unpruned it is eight buds. The larger range in the latter case is due to the smaller population and the necessity of avoiding classes of very low frequencies.

TABLE III.—*Total production of laterals on mother shoots possessing varying number of buds*

Mean number of buds on mother shoots.	Treatment of mother shoots.	Total mean lateral production.	Root-mean-square deviation.
		Cm.	
5	Pruned	246.3	
8	do	269.3	
11	do	240.7	
14	do	245.9	
17	do	237.8	
20	do	237.2	
23	do	246.1	
26	do	313.1	
32	do	281.6	
Mean		257.6	24.22
16	Unpruned	142.6	
24	do	134.1	
32	do	172.5	
Mean		149.7	16.47

It is easily seen from Table III that there is little real difference in the mean total length of laterals on mother shoots of different sizes. In both pruned and unpruned mother shoots it will be seen that, so far as total shoot growth is concerned, there is no marked or consistent difference between the various classes, though there is a tendency for greater growth output on the class of mother shoots possessing from 25 to 27 buds. It will be found, however, that the values are not so widely dispersed from their respective means as to indicate deviations of marked biological significance. In each case the deviation of the

several values from their mean is only about 10 per cent of the mean. In dealing with biological material we should not be justified in attaching any significance to such slight differences, since they might just as probably be due to factors which produce chance variations.

It therefore seems evident from these figures that the growth output of a mother shoot is practically independent of the number of buds it possessed or of the number of laterals it produced. On the mother shoots on the pruned trees the largest number of laterals in the various classes ranged from 4 to 36, nevertheless the total production of laterals was remarkably uniform, considering the variability commonly encountered in biological material. It should be noted that the differences in length of the pruned shoots were due to the varying amounts of wood removed when they were pruned and not to inherent differences in their size.

These results seem to correspond with the data obtained by Miss Brenchley (*1*) on the total dry-weight production of barley and mustard in pots containing uniform quantities of soil. She found that, so far as total dry weight was concerned, there was no real difference whether there were 1, 2, 3, 4, or 5 plants per pot.

In this inquiry we have so far neglected one question which the reader is likely to raise, "Is there any tendency toward compensatory growth following the amputation of various amounts of the mother shoots?" In the category of biological ideas there has been some sort of idea that an injured organism, or one of its members, has a tendency in its growth to "restore lost parts." This idea, though often expressed in crudely anthropomorphic phraseology, has dominated many purely qualitative studies in regeneration. It is deserving of study in a quantitative way if possible.

The total new growth plus the length of the mother shoots may be compared for the different classes of mother shoots. Table IV gives the means of these various sums and the root-mean-square deviation of the series from their respective averages. For the pruned shoots the values range from 260.0 cm. for the "5" class to 381.7 cm. for the "26" class, a difference between extremes of 121.7 cm. The mean total lengths of laterals alone (Table III) had an extreme difference of 75.9 cm. The wider range of values in Table IV is to be attributed to the inclusion of the length of the mother shoots. Another way of showing the same relation is by the value of the root-mean-square deviation which measures the dispersion of the variates from their mean value. In Table III the root-mean-square deviations for the pruned and unpruned shoots were 9.4 and 11.0 per cent of their respective means. In Table IV these deviations were raised to 12.8 and 15.1 per cent of the respective means.

TABLE IV.—*Length of mother shoots plus total length of new wood produced on them*

Mean number of buds on mother shoot.	Treatment of mother shoots.	Length of mother shoot plus total new growth.	Root-mean-square deviation from mean.
		Cm.	
5	Pruned	260.0±14.6	
8	do	293.1±12.6	
11	do	276.5± 8.2	
14	do	288.7±11.6	
17	do	285.0±12.3	
20	do	283.6±11.7	
23	do	307.2±16.1	
26	do	381.7±24.6	
32	do	366.3±23.9	
Mean		304.7±8.79	39.08
16	Unpruned	178.6±10.8	
24	do	185.4± 6.5	
32	do	247.1±14.9	
Mean		203.7±12.0	30.81

The coefficient of correlation between the length of the mother shoots and the total amount of new growth produced by them is a more concise way of expressing the degree of association between the two variables. The values of these coefficients were found to be—

For the unpruned shoots.....$r=0.140\pm0.074$.
For the pruned shoots.....$r=0.004\pm0.041$.

The first coefficient is only twice its probable error and can not be regarded as of much significance, and the second coefficient fails to show any degree of association whatever. It does not appear, therefore, that there is any tendency in these pear trees toward stabilizing the size of the system, mother shoot plus new laterals. In other words, there is no tendency toward a "restoration of lost parts" through growth.

The absence of such a tendency to restore lost parts is also emphasized by the amount of growth produced on mother shoots which received no pruning. Without any stimulus of that sort they produced 58 per cent as much new growth as their pruned neighbors.

RELATIONS BETWEEN THE SIZE AND THE POSITION OF LATERALS ON THE MOTHER SHOOTS

The laterals growing from the buds on a mother shoot exhibit differences which are so characteristic as to attract the attention of the most casual observer. On the pear, as well as other trees, the longest lateral is usually produced at the apex of an upright mother shoot, and each successively lower lateral is usually shorter than the one above it. We may proceed to a study of the quantitative relations of the laterals in this population.

The mean length of the laterals is given in Tables I and II, but it will facilitate the inquiry to have them assembled in basipetal order as in Table V. These means are composites of those in Tables I and II, but in making them due weight was given to the shoot-producing power of each class of mother shoots. The shorter mother shoots were necessarily omitted in making up the means of buds having higher serial numbers. For example, consider a mother shoot which had, after pruning, 14 buds. Obviously this shoot could produce no laterals from the twentieth bud, because it had none. Therefore, it was omitted from all classes having more buds than 14 at the outset. If a mother shoot possessing originally 26 buds failed to produce a lateral from the twentieth bud, its production (for that bud) was counted as zero and the mean was correspondingly influenced.

TABLE V.—*Mean length of laterals produced on mother shoots*

Lateral No.	Pruned.		Unpruned.	
	Observed.	S.	Observed.	S.
	Cm.	*Cm.*	*Cm.*	*Cm.*
Apical	.....	.....	67.76	67.76
I	110.18	110.18	15.49	44.22
II	69.14	70.66	20.67	10.72
III	31.14	40.09	5.94	12.34
IV	11.03	20.08	4.01	4.64
V	9.01	6.43	3.34	3.01
VI	1.82	6.29	2.01	2.74
VII	3.57	1.93	2.13	2.29
VIII	2.04	2.23	2.56	2.22
IX	.88	1.64	2.31	2.69
X	1.23	1.51	2.82	2.27
XI	2.14	2.40	2.22	2.52
XII	3.57	1.85	2.21	2.16
XIII	1.55	2.38	2.09	1.90
XIV	1.18	1.05	1.58	1.63
XV	.55	1.53	1.16	1.11
XVI	1.87	1.44	.63	1.15
XVII	2.32	1.44	1.13	.86
XVIII	1.01	2.53	1.08	.92
XIX	2.73	.62	.71	.89
XX	.22	1.71	.69	.60
XXI	.68	1.06	.48	.53
XXII	1.89	1.77	.37	.44
XXIII	2.85	2.88	.39	.33
XXIV	3.87	2.69	.29	.30
XXV	2.33	3.04	.22	.25
XXVI	2.21	1.52	.21	.22
XXVII	.71	1.11	.22	.11
XXVIII	0	.36	0	.11
XXIX	0	0	0	0
XXX	0	0	0	0
XXXI	0	0	0	0
XXXII	0	0	0	0
XXXIII	0	0	0	0
XXXIV	0	0	0	0
XXXV	0	0	0	0
XXXVI	0	0	0	0

The data presented in Table V show that the lengths of the laterals arranged in basipetal order form some sort of a descending series. The lengths of the first half dozen laterals descend very rapidly; indeed, from that point down there is no marked decrease in values in the pruned series, though the unpruned series shows a second descent from about lateral XVIII. In data of this kind it is frequently advantageous to use S instead of the observed values of y. In this case S is computed from

$$\frac{y_{x-1}+y_{x+1}}{2},$$

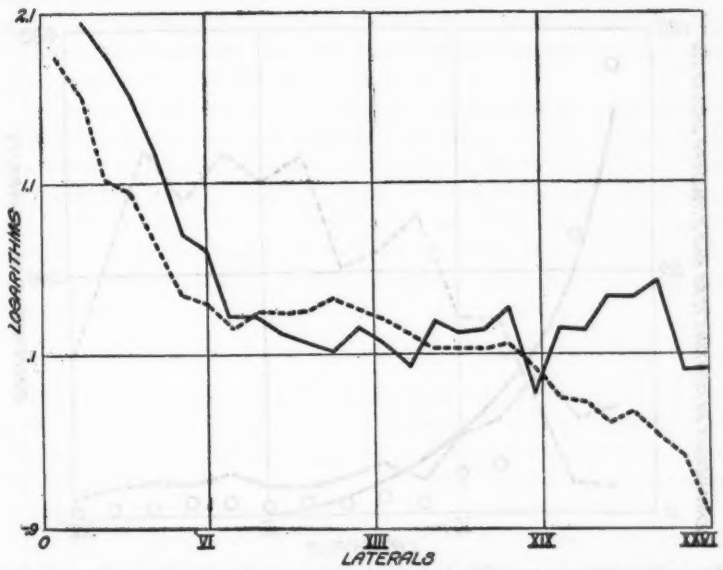

FIG. 3.—Logarithmic values of S (the adjusted value of the mean length of the laterals). The solid line indicates the values for the laterals on pruned mother shoots and the broken line the values for the laterals on unpruned mother shoots.

when y represents length of the lateral and x represents its ordinal position on the mother shoot. Thus the value of S for any given lateral represents the average of the preceding and the following laterals. As McEwen and Michael (*6*) have pointed out, this takes advantage of the fact that the slope of a chord of a simple curve is approximately equal to the slope of the tangent at the point midway between the extremities of the chord. Its use enables one to smooth out inequalities due to errors of sampling or to other causes. In comparing the various values of S it is convenient to employ logarithms of the values, as was done in making the graphs shown in figure 3, because of the wide range of the figures and of the difficulty in using a satisfactory scale. It is obvious that these graphs would descend in a comparatively straight

line from left to right if the lengths of the laterals formed a regularly descending geometrical series. As mentioned above, the descent is by no means uniform. The logarithms of the first seven values of S descend rapidly and somewhat uniformly, but from that point on the descent is less rapid and more irregular. In the language of the horticulturist, the first few buds formed shoots and the rest formed fruit spurs. The formation of these two classes of laterals is of great importance in horticultural practice, and their regulation is one of the principal objects of pruning. A discussion of the physiological aspects of the problem will, however, be postponed until other data have been presented.

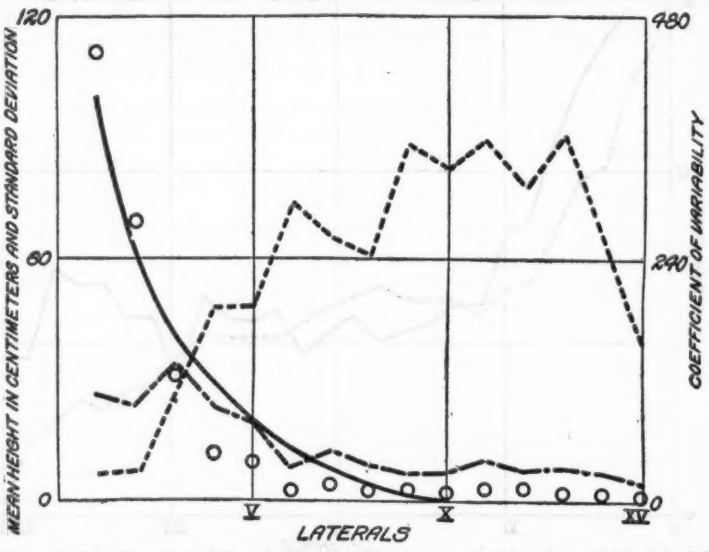

FIG. 4.—Mean length and variability of laterals I to XV on pruned mother shoots. The circles indicate the observed mean lengths of laterals; the dots and dashes, the standard deviation; the broken line, the coefficient of variability of laterals; and the solid line, the mean length of laterals I to X calculated from $y=93.47+4.193x-136.907 \log x$.

The length of the first 10 laterals when plotted as in figure 4 indicates that they follow a curve of a type frequently encountered in biological data. By the aid of tables given by Pearl and McPheeters (*8*) the equation for this curve was computed and found to be

$$y=93.47+4.193x-136.907 \log x,$$

when y represents length of lateral and x represents its ordinal position on the mother shoot. The path of this curve is shown in figure 4. That it is more representative of the laterals than of the fruit spurs is shown both by its shape and by the fact that it gives values of zero or less from lateral X and below.

These figures clearly betoken certain biological relationships which must be of prime importance in attempting to understand the laws of development in higher organisms. They make it possible to extend the ideas on integration and differentiation which formed such a considerable part of Herbert Spencer's (*13*) "Principles of Biology." The figures presented show that the length of a lateral is some sort of a function of its ordinal position on the branch which bore it. That the length of a given lateral is as much an expression of the properties of the branch as the angles of a crystal are of the properties of a salt there can be no reason to doubt. This is not to say that the equation giving the length of a lateral will necessarily disclose the physiological factors determining it, but it does banish the idea that form and function are so variable as to be outside of the realms of exact science.

The series of correlations reported on a subsequent page are further evidence of a functional relationship between the various laterals with due regard to the factors which may reside in the mother shoot. The representation of their relative length by a mathematical equation is not, therefore, due to chance or to the fortunate choice of an equation. Future work in this important field on subjects such as those investigated by Pearl (7) and by Johnson (*4*) should afford information of the utmost value.

VARIABILITY IN THE LENGTH OF LATERALS

The biological constitution of the population under consideration was next investigated. The nature and amount of variability existing in the population was used as an indicator of its genetic character. The laterals on the pruned shoots served as a basis for the inquiry, because of the larger number in the population.

A graph in figure 4 shows the coefficient of variability of the first 15 laterals produced on the pruned mother shoots. The coefficients of variability of these means increases somewhat irregularly from 23.18 for lateral I to 359.90 for lateral XIII and falls to 159.52 for lateral XV. This indicates that the laterals produced from the distal end of the mother shoot are less variable in length than those produced nearer the proximal end of the shoot. This increased variability can not be attributed to the smallness of the group or to a poor sample, because lateral XIII comprised a population of 172 individuals.

The fact that minimum variability occurs in the members at the distal end of the shoot has previously been noted in Ceratophyllum (7). On Ceratophyllum the whorls of leaves borne at the distal end of the shoot may be considerably younger than those borne at the opposite end. On the pear shoots the distal lateral is likely to be the oldest on the mother shoot, though in many cases the difference in age is very slight. The position of the lateral upon the parent axis appears to be more of a factor than age in determining variability in length.

Another phase of the variability of the laterals is shown by the graphs in figure 5, which show the frequency distributions of laterals I and V in the pruned class and of the apical shoot in the unpruned class. The graphs for the apical lateral in the unpruned class and for lateral I are fairly symmetrical but have a skewness in the direction of the higher values. The graph for the lateral V is very asymmetrical because a disproportionate number of variants fall in the upper classes. Each of these graphs indicates that the variability in the length of the laterals is not a chance phenomenon, but that it is a function of their position on the mother shoot. The tendency of these factors is to produce more long laterals in each class than would be found if their length were

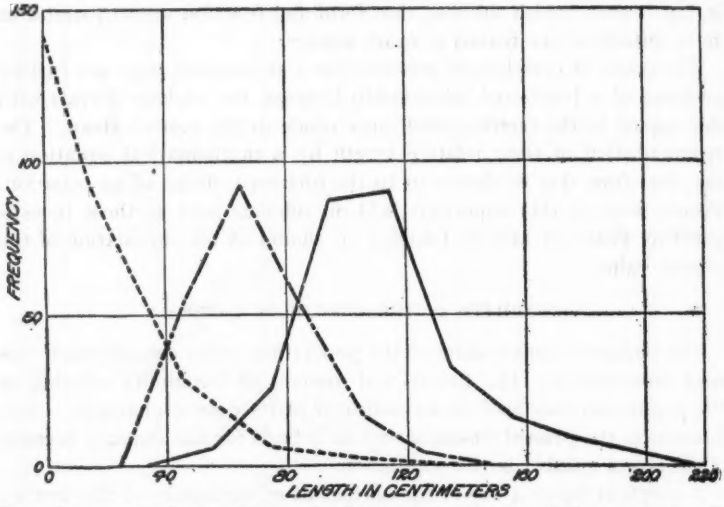

FIG. 5.—Frequency distributions of the mean lengths of certain laterals. The solid line represents lateral I on pruned mother shoots; the broken line, lateral V on pruned mother shoots; and the dots and dashes, the apical lateral on unpruned mother shoots.

determined by pure chance. That this influence is inherent in the tree and not due to the operation of pruning is shown by the same tendency in the frequency distribution of the laterals arising from the apical buds on the unpruned mother shoots.

II. DOMINANCE OF THE DISTAL LATERALS OF THE PEAR TREE

It is hardly necessary to mention again that the distal lateral on a vertical shoot is usually larger than any other lateral growing between it and the base of the mother shoot. It will be profitable to study the problem somewhat further with the hope of gaining more light on the causes of this characteristic type of growth.

An inspection of the tables giving the size of laterals on the mother shoots shows that, as a rule, the length of the distal lateral has some sort of inverse ratio to the length of its mother shoot. The relationship was determined by computing the coefficient of correlation between

the length of the distal laterals and the number of buds possessed by the mother shoots upon which each was produced. The number of buds is thought to be of greater biological significance in this case than the actual length of the mother shoot. The value of this coefficient for the pruned shoots is $r = -0.266 \pm 0.038$, and for the unpruned -0.196 ± 0.088. The negative coefficients are in harmony with the relations already observed between mother shoots and their distal laterals. The coefficient expressing the negative correlation between the length of the pruned mother shoots and their distal laterals is statistically significant and indicates that the more severely the mother shoots were pruned

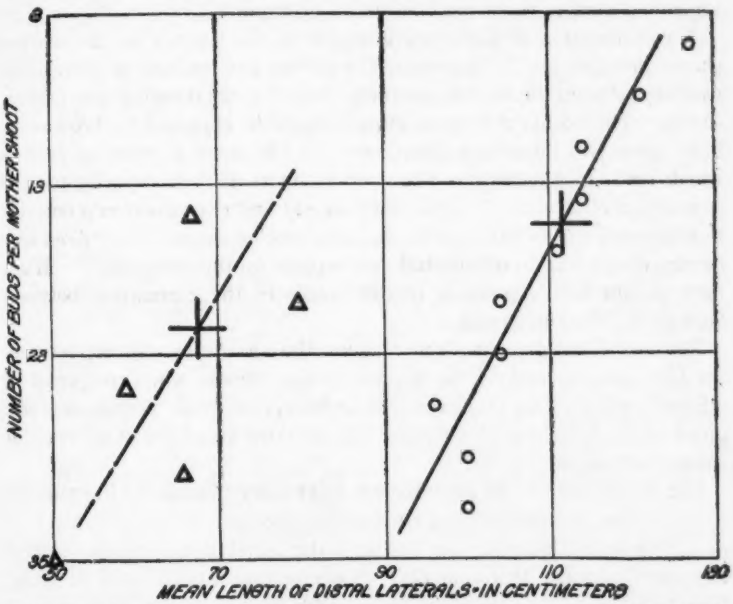

FIG. 6.—Regression of mean length of distal laterals on mean number of buds per mother shoot. Circles indicate observed mean length of laterals on pruned mother shoots; the solid line, the curve of means calculated for laterals on pruned shoots; the triangles, the observed mean length of laterals on unpruned mother shoots; and the broken line, the curve of means calculated for laterals on unpruned mother shoots.

the longer were their distal laterals. For the unpruned mother shoots the correlation coefficient is likewise negative, but statistically less reliable because of the relatively large probable error accompanying it. Had the calculations been based upon a larger population, this coefficient might have been closer to that for the other class of shoots.

The regression of the means in the two cases is shown in figure 6. The calculated values were obtained from the formula

$$X = \left(\bar{x} - r\frac{\sigma_x}{\sigma_y}\bar{y}\right) + \left(r\frac{\sigma_x}{\sigma_y}\right)y,$$

where $\bar{x}$ is the mean value of the x's, $\bar{y}$ of the y's, and r is the correlation coefficient.

We may digress momentarily to see whether the pruning increases the dominance of the laterals produced in the distal region of the mother shoot. For example, in Table I it will be seen that the class of mother shoots having 23 original buds produced a mean total shoot growth of 242.5 cm. and that the five upper buds produced 90.7 per cent of the total shoot wood. By comparing this with unpruned mother shoots having 24 original buds (Table II), it will appear that the five upper buds produced only 78.8 per cent of the total shoot growth. It will also be noted that 21 laterals were produced on the average pruned mother shoot mentioned, and 25 laterals were produced on the average unpruned mother shoot selected as an example.

A consideration of the relative length of the laterals on the mother shoots prompts one to determine the nature and amount of correlation existing between the laterals produced near the distal end of the mother shoots. The results of such an inquiry might be expected to throw some light upon two important questions—(1) "Is there a group of factors which tends to differentiate the mother shoots in their capacity for the production of laterals?" If so, they should find expression in a correlation between any two laterals on the same mother shoot. (2) "Are there factors which tend to differentiate the laterals on the same axis?" If so, they should find expression in differences in the correlation between laterals in different positions.

The coefficients given in Table VI show the correlation existing between the first four laterals on the pruned mother shoots when compared in different ways. The coefficients of ordinary, or gross, correlations are given at the head of each column. Below them stand the coefficients of partial correlation.

The latter coefficients are intended to express adequately the amount of correlation existing between nonadjacent shoots. They are an attempt to answer such a question as, "What is the correlation between the first and third laterals, assuming that all the second laterals were of equal length?"

TABLE VI.—*Coefficients of gross and partial correlation of the length of the four distal laterals on pruned mother shoots*

r_{12}	0.346±0.036	r_{13}	0.296±0.037	r_{14}	0.157±0.040
$r_{12.3}$	.266± .038	$r_{13.2}$	.211± .039	$r_{14.2}$	.090± .041
$r_{12.4}$	.324± .037	$r_{13.4}$	.267± .038	$r_{14.3}$	.083± .041
$r_{12.34}$	.258± .038	$r_{13.24}$	.197± .039	$r_{14.23}$	.046± .041
r_{23}	0.313±0.037	r_{24}	0.216±0.039	r_{34}	0.272±0.038
$r_{23.1}$	.235± .039	$r_{24.1}$	.175± .040	$r_{34.1}$	.239± .039
$r_{23.4}$	.270± .038	$r_{24.3}$	.143± .040	$r_{34.2}$	.221± .039
$r_{23.14}$	.202± .039	$r_{24.13}$	.126± .040	$r_{34.12}$	.207± .039

The coefficients of gross correlation are all positive and of sufficient magnitude in comparison with their probable errors to be considered significant. They indicate that the growth of one lateral is correlated

with the growth of other laterals on the same mother shoot and that the correlation between adjacent laterals is greater than for nonadjacent laterals, suggesting that the factors determining the amount of growth are not uniformly distributed in the mother shoots. Moreover, the greatest correlation is found between laterals at the distal end of the mother shoots and becomes less with each successively lower pair of laterals.

The coefficients of partial correlation go somewhat further in showing these relations. A comparison of r_{12}, $r_{12.3}$, and $r_{12.4}$ shows that by equalizing the effect of the third lateral, the coefficient is diminished from 0.346 to 0.266, but equalizing the effect of the fourth lateral reduces it only from 0.346 to 0.324. Broadly speaking, the length of the fourth lateral has less effect than that of the third upon the correlation between the length of the first and second laterals. When the length of both the third and fourth laterals is equalized the correlation between the first and second laterals is reduced from 0.346 to 0.258. The value of r_{14} is the lowest of all the gross correlations and the coefficients of partial correlation into which r_{14} enters are so low in comparison with their probable errors as to lack statistical significance.

The values of these coefficients may, therefore, be regarded as good evidence in favor of an integral relationship in the growth processes of neighboring laterals on an upright mother shoot and that neighboring laterals have a tendency to vary together. It would seem difficult to escape the conclusion that factors which promote growth in any lateral also tend to promote growth in the adjacent lateral. It would at least seem that these measurements speak against any explanation which rests upon the assumption that the dominant apical shoot is such because it has withdrawn food or growth stimulators from the subapical region of the mother shoot. It is quite possible that two distinct groups of factors are operating to influence the growth of these laterals, one of which tends to make all the laterals of a given mother shoot either longer or shorter than the average for the population as a whole, while the other group tends to oppose the development of the subapical shoots, this suppression being the more complete as the distance from the distal end of the shoot increases. The existence of significant positive correlations between adjacent laterals speaks for the existence of the first group of factors. The systematic differences in the values of the interlateral correlation coefficients speak in favor of the second group of factors.

This may mean that while there is a well-marked tendency for the factors which produce length in the first lateral to produce length in the laterals below it, there is some other factor at work which tends to block the operation of the length-producing factor in the subapical shoots and that it is more completely blocked as one proceeds down the axis of the mother shoot.

Further light on these questions may be obtained if we inquire concerning the possibility that any lateral may grow to the length of the lateral immediately above it. By use of a formula given by Harris (*3*) we may obtain a quantitative expression of this capacity of subapical laterals to come to development. The capacity of the second lateral to develop with respect to the first might be expressed as

$$r_{xz} = \frac{r_{xy} - \frac{V_x}{V_y}}{\sqrt{1 - r^2_{xy} + \left(r_{xy} - \frac{V_x}{V_y}\right)^2}},$$

where r_{xy} is the coefficient of correlation between the two characters and V_x and V_y are their coefficients of variability.

Determination of these constants gives the following:

Lateral II with respect to lateral I -0.883 ± 0.009.

Lateral III with respect to lateral II -0.876 ± 0.010.

Lateral IV with respect to lateral III -0.830 ± 0.013.

Lateral III with respect to lateral I -0.973 ± 0.002.

Lateral IV with respect to lateral II -0.958 ± 0.003.

Lateral IV with respect to lateral I -0.991 ± 0.001.

These coefficients measuring the correlation between the length of the subtending lateral and the deviation of the variables from their probable values are all negative and relatively large. Their values have a tendency to increase as the distance between the laterals increased.

The results show that the subtending laterals fail to attain the size we should expect when the more distal laterals have a larger size. In short, there is the clearest evidence of a competition, or of an inhibition of growth, associated with the development of the higher laterals.

III. PRODUCTION OF FRUIT SPURS

The short, spur-like branches on the limbs of the pear and other trees call for special consideration. They differ from the longer pliable shoots of the same tree in being primarily fruit-bearing shoots and, in the parlance of the horticulturist, are called "fruit spurs." As is well known, they grow slowly in length, have short internodes, and characteristically bear a flower bud at the apex instead of a vegetative bud. The fundamental physiological and morphological differences between the two classes of shoots have been clearly set forth by Vöchting (*14*) and others.

If we grant that the production of fruit spurs, as well as that of the longer laterals, is a function of the growth process of the tree, we may proceed to inquire concerning their distribution and the laws of their characteristic growth. The difference between fruit spurs and purely vegetative shoots, as mentioned above, is primarily one of degree and not of kind. Consequently it is necessary to fix, arbitrarily, the length

limit which shall define a fruit spur. In this investigation of young branches the limit has been set at 5 cm., and, in accordance, all shoots having a length of 5 cm. or less are designated as fruit spurs.

The number of fruit spurs on the pruned mother shoots ranged from 0 to 13. The larger number were naturally found on the longer mother shoots. The energy of the shorter mother shoots appears to have been used mainly for the production of vegetative shoots. The number of fruit spurs on the unpruned mother shoots ranged from 1 to 20, but only two shoots had fewer than 4 fruit spurs.

The data given in Table VII show the mean number of fruit spurs produced on mother shoots of various classes. The mean spur production of the shorter pruned mother shoots is very low, but increases, somewhat irregularly, until the largest number is found on the mother shoots having more than 28 buds. There is a well-marked tendency, however, to less variability in spur formation on the longer mother shoots. The last two classes of mother shoots on the pruned trees seem to be in a class somewhat different from the others in respect both to the mean number of fruit spurs formed and in having much less variability with respect to the mean. It would seem that these pruned mother shoots failed to produce more than a minimum of fruit spurs except when they possessed more than 25 buds per mother shoot.

The mother shoots on the unpruned trees produced considerably more fruit spurs than their pruned neighbors. The lowest average in this group was practically equivalent to the highest average among the pruned trees. The variability in the number of fruit spurs with respect to their mean was less in the longest mother shoots than in those of any other class. Clearly there is a manifest tendency for decreased variability to be associated with increased production of fruit spurs. This characteristic may also be discerned in the growth of vegetative laterals at least so far as their length is concerned. The greatest output of growth material leads to the production of the longest laterals and to the lowest variability.

TABLE VII.—*Variability in the production of fruit spurs on mother shoots*

Number of original buds on mother shoot.	Treatment of mother shoot.	Mean number of fruit spurs per mother shoot.	Coefficient of variability.
4 to 6	Pruned	0.75±0.20	135.71±40.38
7 to 9	do	.78± .13	142.31±27.00
10 to 12	do	2.53± .18	78.26±10.82
13 to 15	do	2.23± .37	163.23±29.82
16 to 18	do	3.60± .34	93.89±11.07
19 to 21	do	2.52± .29	98.41±13.97
22 to 24	do	2.67± .41	119.10±21.42
25 to 27	do	5.07± .51	57.79± 9.24
28 and more	do	7.88± .69	38.83± 7.47
12 to 19	Unpruned	7.33±1.52	141.40±32.83
20 to 27	do	12.15± .64	40.00± 4.32
28 to 36	do	15.86±1.14	28.32± 5.48

The graphs in figure 7 show the distribution of fruit spurs on two classes of mother shoots, one of which was typical of the pruned and the other of the unpruned shoots. They show that the types of distribution in the two cases are fundamentally different. For the pruned shoots the greatest frequencies were observed for those having 3 fruit spurs or less. For the unpruned mother shoots there were none having less than 4 fruit spurs, and the highest frequencies were found for shoots having 12 to 18 fruit spurs.

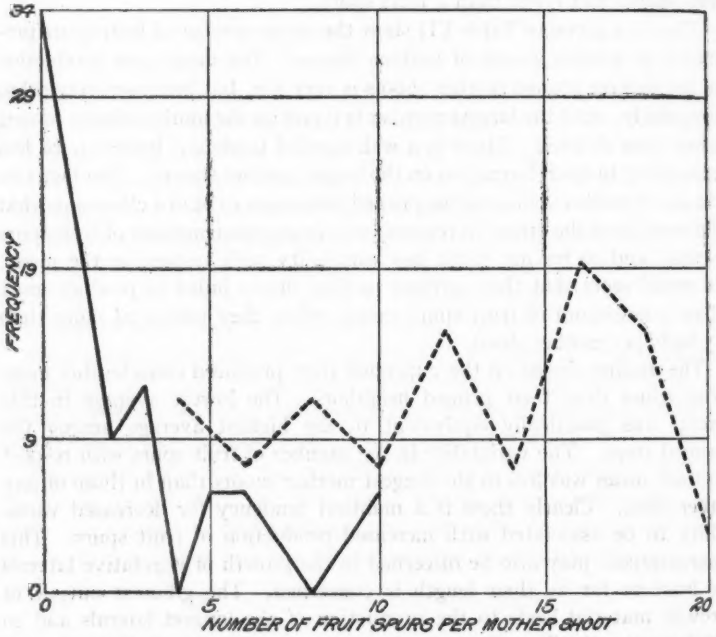

FIG. 7.—The distribution of fruit spurs on two classes of mother shoots of approximately equal length. (Frequencies are expressed as percentages of *n*.) The solid line indicates the distribution on principal mother shoots having 19, 20, or 21 buds and the broken line the distribution on unpruned mother shoots having 20 to 27 buds.

We may say, therefore, that the typical pruned mother shoot was characterized by few fruit spurs and that the typical unpruned mother shoot was characterized by relatively many fruit spurs.

The foregoing statements may appear to contain nothing especially new to those familiar with the art of pruning. They do furnish, however, quantitative data upon which an analysis of the growth response of the tree may be based. Horticulturists have long known that little or no pruning results in the production of shorter laterals and of more blossoms. Whether the tree is thereby rendered more productive or whether the fruit is of satisfactory quality is, however, another question.

DISCUSSION

It remains to see how the data presented above will contribute to an understanding of the growth process in trees, especially in relation to the characteristic formation of vegetative and fruit-bearing shoots. It hardly requires further discussion to show that the new shoots on the pear tree arise in such a perfectly definite and orderly fashion as to suggest that their growth and distribution is governed by definite causal factors. The problem is to discover, if possible, these causal factors and their functions. The discussion will adhere in a general way to the arrangement of data presented in the preceding pages.

The total amount of new shoot material produced on pruned and unpruned mother shoots ought to show what result the stimulus of pruning may produce, and to give a basis for discussing the nature of accelerated growth.

A comparison of the amount of new growth produced in the two cases shows that the branch system is larger at the end of the season than would be required if the growth response were merely a means of restoring what had been removed by pruning. In other words, the amputation of part of the mother shoot has resulted in producing more new growth on what remained of that particular shoot than would have been produced if it had remained uncut. The problem is not, why such a shoot produces new laterals, but why it produces a mass of new laterals about 65 per cent greater than it would if left unpruned. Since this problem is fundamental to the theory and practice of tree pruning, it may be profitable to extend the inquiry as far as possible.

The simplest conception of growth which we seem warranted at present in holding is that it is the result of some sort of a catalyst acting upon substances acquired by, or produced in, the organism. In the absence of contrary evidence we must believe that all buds and other meristematic tissues are supplied with either the active or the potential catalyst. The ratio between the growth of a particular organ and the growth of the rest of the tree must in some way depend upon the relative activity of the catalyst of these organs.

In connection with these suggestions reference may be made to a paper on the growth of pruned and unpruned branches of the apricot tree (*9*). As a result of the pruning the final mean length of new shoots was 210 cm., while it was 94 cm. on the unpruned neighboring trees. The equation for the growth of these apricot shoots was that of a monomolecular chemical reaction,

$$x = a\ (1 - e^{-kt}),$$

in which x represents the length of the shoot at time t, a is the final length of the shoot, k is a constant, and e is the base of the natural logarithms. Having the values of a and k, it is possible to compute the length of the shoots for any value of t in the growing season. For these apricot shoots

the value of k was the same, but that of a differed in the two equations. The rate of growth in such a case is expressed by the differential equation

$$\frac{dx}{dt}=k\ (a-x)$$

or,

$$\frac{dx}{dt}=k\ a\ e^{-kt}.$$

The rate of growth of the shoot appears, therefore, to be dependent upon its final length. The rate may be affected by (1) a variation in the activity of the catalyst or (2) a variation in the supply of potential growth materials. The case of the apricot shoots is believed to be applicable to the pear shoots.

It is difficult to understand how the amputation of a greater or less portion of a mother shoot can increase the supply of potential growth material for the same except as it decreases the number of meristematic centers. Two arguments against the validity of such an assumption at once arise. In the first place, mother shoots which had been pruned produced more new material than unpruned mother shoots possessing the same number of buds (Table III). In that case the number of competing growth centers was the same, but the results were different. In the second place it has already been shown that the number of buds left on a pruned mother shoot had very little effect upon the total amount of new shoot wood produced. The deviation of the values from their mean was less than 10 per cent of the mean.

We, therefore, seem to have reason to assume that the cause of the increased growth is to be referred to an increased activity of the growth catalyst. The reason for this increased activity will be discussed in connection with the difference in growth of the several laterals.

If no opposing factors were operative we should expect that each mature bud on the mother shoot would develop into a lateral shoot. The size of the laterals would be largely determined by the amount of energy which they were able to obtain from the parent tree supplemented by what they could obtain from outside sources. To state it somewhat more specifically, the size of a young lateral at the outset would depend upon the amount of growth-promoting material which the parent tree could furnish it. In course of time, however, the assimilatory system of the new shoot would be able to furnish additional supplies of material, a part of which could be used to further the growth of that shoot. The amounts of growth-promoting materials obtained in the latter, as well as in the former, case would largely be determined by the position of the shoot, which would in turn determine the conditions of competition for water, light, and other factors. The buds near the base of the mother shoot might, therefore, be expected to grow first into shoots and subsequently to develop as their access to light should give them opportunity.

The most casual observer is aware, however, that the lateral shoots arising from an older vertical shoot are by no means equal in length. The longest lateral is usually produced at the apex of the mother shoot, and each successive lateral is shorter than the preceding.

This characteristically greater growth of new shoots at the distal end of an upright branch, especially after pruning, is a well-recognized condition. An adequate understanding of its causes is greatly to be desired. Many of the statements on the subject to be found in botanical literature are vague, and others are mystifying. For example, the mere statement that "the available food materials of the stem are principally devoted to the development of the apical bud" raises more questions than it answers. The statement that the growth on an upright branch is regulated by polarity falls into the same category. In the sense that "polarity" has been applied to the formation of shoots and roots on cuttings this idea would be inapplicable to the factors influencing fruit-spur formation, since, in its implication, "polarity" involves the idea of two mutually exclusive, opposite qualities—for example, the opposite ends of a magnetized bar of metal. The idea of an "axial gradient" as used by Child (*2*) is a more exact designation of the phenomenon but does not account for the production of the gradient. If it be solely a question of the distribution of nutrient materials in the parent branch it is difficult to understand why the growing points at the distal extremity of the branch should acquire such quantities as would result in the production of larger shoots, while the growing points near the proximal extremity usually fail altogether to develop into shoots in the first season.

It seems logical to assume that the type of development observed depends not upon the distribution of nutrient materials in the parent branch but upon the distribution of some substance which is antagonistic to growth. This substance may be formed in the distal region of the shoot and migrate toward the base of the shoot. Certain evidence on this point has been already presented (*11*). We may, therefore, assume that the amputation of a portion of the mother shoot—removing the apical bud and a number of adjacent subapical buds—removed the most active centers in which some sort of a growth-inhibiting substance was produced. The effect of this operation was to remove an obstacle which impeded the development of subapical buds into shoots. This is an aspect of the theory of chalones which are recognized as factors in the growth of the animal body and which have been discussed in relation to plant growth by Loeb (*5*) and Reed and Halma (*10*, *11*). On the basis of this assumption it would appear that the buds immediately below the point of amputation grow first because they are the first to be freed from the inhibiting substance. As soon as the new shoots begin to grow they begin to produce more

of the inhibiting substance, which, in turn, tends to keep the buds below them dormant. The successively smaller size—diminishing length— of the lower shoots appears to be due to the effect of the growth-inhibiting substance produced in those above, an effect to which each shoot contributes, with the result that the lowest buds are entirely prevented from developing.

We may proceed to examine the plausibility of these theories as applied to the formation of laterals. On the supposition that a reduction in the length of the mother shoots so reduces the demands on the resources at the disposal of the tree that each growing point acquires a larger supply of these resources we should expect that the shorter mother shoots would produce more lateral growth than the longer mother shoots. Reference to the total lateral growth of the different mother shoots shows that this was not the case. If any difference existed it was in favor of the longer mother shoots. If we compare two classes of mother shoots originally possessing approximately the same number of buds, one of which was pruned and the other unpruned, we shall see that the pruned mother shoots produced considerably more total growth than the unpruned. A possible objection to this comparison may be mentioned—the shoots which were pruned were constitutionally more vigorous, because after removing a portion they were still as long as a certain class of unpruned mother shoots. An examination of Table III shows, however, that there is no ground for this objection, because the longest unpruned mother shoots failed to produce as much lateral growth as the shortest pruned shoots. The objection may, therefore, be dismissed.

An inspection of the trees in the orchard would convince any impartial observer that the pruned trees were in no way inferior in size to the unpruned, although the shape of the tree naturally differs. After three years the trees receiving heavy pruning each winter—the trees on which the pruned mother shoots were selected for measurement—had an average trunk girth of 16.2 ± 0.3 cm., and the unpruned trees had a girth of 16.6 ± 0.2 cm. Obviously the difference between the two is negligible.

Passing to the second possible explanation, that of an inhibitor, we should expect to find that the removal of the apical bud of a shoot, or of the zone in which the inhibitor was principally produced, would be shown by greater growth of laterals from the shoot remaining. So long as the principal source of the inhibitor were removed the total amount of new growth would have little, if any, relation to the length of the mother shoot until new supplies were produced. The data give strong evidence in favor of such an assumption. As soon as growth of the new lateral got underway more of the chalone would be produced and would inhibit growth in the subapical laterals so that total lateral growth would be limited and would diminish with the distance of the laterals from the apex of the mother shoot.

It would also appear that the data fail to support the assumption that in such cases a growth-stimulating substance migrates from the surrounding tissues and accumulates in the dominant area. It is quite probable that the growth-stimulating substances are of the nature of catalysts but that they occur in all buds on a mother shoot. We know that the amputation of a portion of a pear shoot will be followed by the growth of laterals from the buds immediately below the point of amputation (*10*). The data here presented show that the first laterals from the shorter mother shoots were longer than those from the longer mother shoots. Yet the latter had a larger surrounding area to draw upon if we assume that the growth of laterals was governed by the migration of growth-promoting substances. Furthermore, the slope of the regression line (fig. 6) indicates that the relationship between length of mother shoot and length of first lateral is negative throughout the whole population.

In order to remove a possible confusion in the mind of the reader, the substance of previous paragraphs may be repeated at this point. The shorter mother shoots, although producing longer apical laterals, nevertheless produced practically the same total of laterals as the longer mother shoots.

It would seem more logical to assume that each of the buds on the mother shoot is provided with the growth-stimulating substance (catalyst) and that all will grow provided they are sufficiently freed from substances which inhibit the action of the catalyst.

SUMMARY

(1) The paper contains an attempt to analyze and correlate the growth phenomena of young shoots on branches of the pear tree.

(2) Mother shoots which had been headed back in the previous winter produced about 65 per cent greater total growth of laterals than their unpruned neighbors. The frequency distributions of laterals on both classes of mother shoots show a positive skewness, which is taken to indicate a tendency to produce more than the mean quantity of wood.

(3) If mother shoots received any pruning whatsoever, the severity of the pruning seemed to have little influence upon the total amount of new laterals produced in the following season. The growth response showed little tendency toward a "restoration of lost parts."

(4) The longest lateral on a mother shoot is usually at the distal end, and each successively lower lateral is usually shorter than the one above it. The mathematical relationships of the system of laterals indicate a definite functional relation of the growth processes involved. Variability in the length of laterals tends to increase as their distance from the distal end of the mother shoot increases.

(5) The lateral arising from the distal end of an upright mother shoot exerts a well-marked dominance over those arising from buds beneath it. The mother shoots which were most reduced in length by pruning usually produced longer distal laterals.

(6) There is a well-marked positive correlation in the length of neighboring laterals on the same mother shoot, but the correlation diminishes as the distance between the points of origin of the laterals increases; that is to say, the longer the distal lateral becomes the more will the subtending laterals fall short of the size which they might be expected to attain from the general size relations in the population under consideration. In harmony with such a relationship, it was found that the capacity of any lateral to reach the length of a lateral situated higher on the mother shoot is expressed by a relatively large negative coefficient.

(7) Fruit spurs were commonly more abundant upon unpruned mother shoots than upon those receiving pruning in the previous winter.

(8) The growth response indicates that increased growth following pruning is due to the removal of regions containing, or producing, substances which would otherwise tend to inhibit growth of other members of the system. Each mature bud on the mother shoot seems capable of developing into a lateral provided it be sufficiently free from growth-inhibiting substances.

(9) On the assumption that the pear branches produce a growth-inhibiting substance which flows in a basipetal direction, it is logical to find a gradient in the formation of laterals such as that existing here. The inhibitor would be more concentrated as the distance from the apex of the shoot increased. The effect of the increasing concentration would be to retard increasingly the growth of the lower laterals until finally such a concentration would be reached as to inhibit growth entirely. In this way the dominance of the apical shoots would be not only established but perpetuated.

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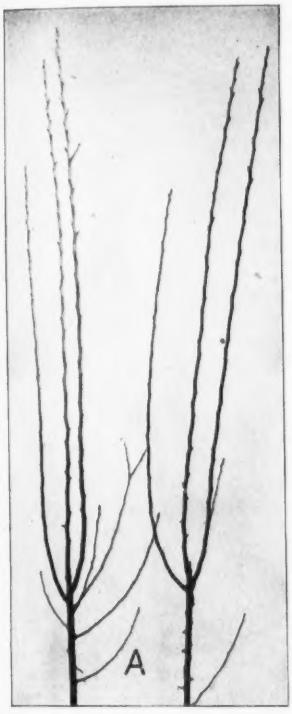
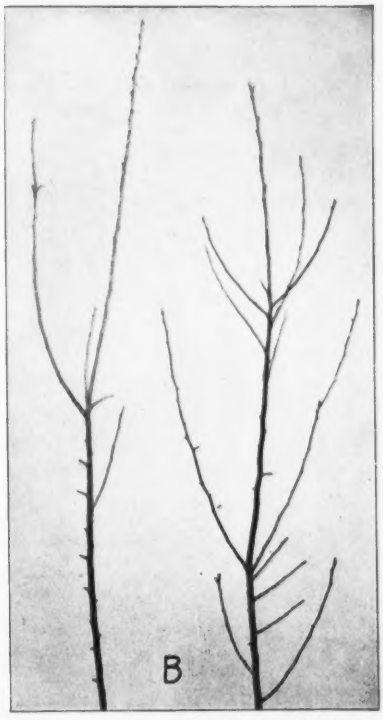
Plate 142.

Examples of pruned and unpruned mother shoots with laterals at end of growing season.

A.—Pruned.

B.—Unpruned


A


B

INDEX

Page

Abies—
apollonis, effect of iron sulphate on chlorosis. 154
balsamea, effect of iron sulphate on chlorosis 154
bicolor, effect of iron sulphate on chlorosis... 154
pectinata, growth on calcareous soil..... 154
Acid—
citric, production by storage-rot fungi..... 223
oxalic, production by—
Sclerotinia cinerea..... 631
storage-rot fungi..... 223
phosphoric, in urine, effect of cucurbita seeds..... 525–528
sulphuric, in urine, effect of cucurbita seeds..... 525–528
Acid producers in silage..... 769–770
Acidity—
of silage..... 771
of urine, effect of cucurbita seeds..... 524–528
Acids—
organic, produced in respiration of storage-rot fungi..... 222–223
production by *Rhizopus tritici*..... 631
Acremonium sp., isolated from potatoes..... 828
Actinomyces—
bovis, failure to produce odor on beef..... 695
chromogenus, effect of hydrogen-ion concentration on growth..... 202
Aethecerus n. sp., parasite of *Recurvaria milleri*..... 138
Agglutination tests of *Bacillus megatherium*.. 696
Agropyron repens, indeterminate rhizome.... 177
Agrostis alba, determinate stolon..... 177
Albumen, black blood, in ration for pigs... 281–341
Albumin, milk, in ration for pigs..... 281–341
Albuminoid nitrogen in silage..... 771
Alcohol—
in silage..... 787
produced in respiration of storage-rot fungi..... 221–222
Alfalfa. See *Medicago falcata*.
Alkali, effect on permeability of soil..... 265–278
Alternaria—
sp., isolated from potatoes..... 828
tenuis, glucose as a source of carbon..... 189–210
Amino nitrogen in silage..... 772
Ammonia—
in silage..... 787
nitrogen in silage..... 772
Ammonium—
hydrates in urine, effect of cucurbita seeds..... 524–528
nitrate, effect on growth of storage-rot fungi 190
sulphate, effect on plants supplied with iron..... 701–728
Anastatus semiflavidus—
description..... 374–375
distribution..... 373
habits..... 380–383
hosts..... 383–384
life history..... 375–378
parasite of *Hemileuca oliviae*..... 373–384

Page

Anemia, equine, blood counts..... 684–688
Angitia sp., parasite of *Recurvaria milleri*.... 138
Anthelmintic properties of carbon tetrachlorid..... 157–175
Anthony, Stephen, and Harlan, Harry V. (paper): Effect of Time of Irrigation on Kernel Development of Barley..... 29–45
Apanteles n. sp., parasite of *Recurvaria milleri*. 138
Aphids, transmission of leafroll..... 53–59
Aphis—
potato. See *Macrosiphum solanifolii*.
spinach. See *Myzus persicae*.
Apium graveolens, host of *Pseudomonas apii* 185–188
Aplanobacter stewarti, Stewart's disease of corn..... 263–264
Appleman, Charles O. (paper): Reliability of the Nail Test for Predicting the Chemical Composition of Green Sweetcorn..... 817–820
Apricot trees, concentration of cell sap.. 85–86, 94–95
Armsby, Henry Prentiss, and Kriss, Max (paper): Some Fundamentals of Stable Ventilation..... 343–368
Arny, A. C. (paper): Further Experiments in Field Technic in Plot Tests..... 483–500
Ascarids, efficacy of carbon tetrachlorid against..... 157–175
Ascaris equorum, relation to Eosinophiles.. 679–688
Ash—
effect on development of pigs..... 280–341
in barley kernels, effect of time of irrigation 31–45
stored on different rations..... 326–334
Aspen. See *Populus tremuloides*.
Aspergillus—
glaucus, glucose as a source of carbon..... 189–210
niger—
glucose as a source of carbon..... 189–210
sugar used in respiration..... 218
Assimilation of Nitrogen, Phosphorus, and Potassium by Corn when Nutrient Salts are Confined to Different Roots (paper).. 545–573
Austrian pine. See *Pinus austriaca*.
Awns, suppression by fungus..... 699–700
Bacillus—
bronchisepticus, failure to produce odor on beef..... 695
carotovorus, enzym production..... 611–612
casei, ability to produce ammonia..... 787
coli—
communior, failure to produce odor on beef..... 695
communis, failure to produce odor on beef 695
glucose as a source of carbon..... 189–210
enteritidis, failure to produce odor on beef.. 695
gallinarium, failure to produce odor on beef. 695
icteroides, failure to produce odor on beef... 695
lactimorbis, failure to produce odor on beef. 695
lathyri, causal organism of "stripe" disease of tomato..... 123
megatherium—
cause of souring of beef..... 689–698

Page

Bacillus—Continued.
var. *de Bary*, similarity to *B. megatherium* var. *Ravenellii*..... 691-698
var. *Ravenellii*, similarity to *B. megatherium* var. *de Bary*..... 691-698
mesentericus, failure to produce odor on beef 695
omnivorus, enzym production..... 611
phytophthorus, prevention of infection by wound-cork formation..... 646
prodigiosus, failure to produce odor on beef.. 695
pullorum, failure to produce odor on beef.. 695
pyocyaneus—
failure to produce odor on beef..... 694
glucose as a source of carbon..... 189-210
subtilis—
failure to produce odor on beef..... 695
glucose as a source of carbon..... 189-210
typhi murium, failure to produce odor on beef..... 695
vulgatus, odor on beef..... 695
Bacillus, grass, of Moeller, failure to produce odor on beef..... 695
Bacillus of Priesz and Nocard, failure to produce odor on beef..... 694
Bacterial Budrot of Cannas, A (paper)..... 143-152
Bacterial Leafspot Disease of Celery (paper) 185-188
Bacterial Spot of Tomato (paper)..... 123-156
Bacterial Wilt of Castor Bean (Ricinus communis L.) (paper)..... 255-262
Bacteriological and Chemical Studies of Different Kinds of Silage (paper)..... 767-789
Bacterium—
cannae, n. sp.—
distribution..... 146
organism..... 148-152
susceptible hosts..... 145
exitiosum, n. sp.—
causal organism..... 130-155
hosts..... 123-125
relation to bacterial spot of pepper..... 125-126
symptoms..... 126-129
technical description..... 141
temperature relations..... 138-139
fumefaciens, inoculations on *Bryophyllum calycinum*..... 593-598
vesicatorium, n. sp. See *Bacterium exitiosum*, n. sp.
Balsam. See *Impatiens balsamina*.
Barley. See *Hordeum* spp.
Bean, castor. See *Ricinus communis*.
Beans, varietal susceptibility to rust..... 385-404
Beef, souring..... 689-698
Beetle, mountain-pine. See *Dendroctonus monticolae*.
Bermuda grass. See *Cynodon dactylon*.
Biological Study of the Red Date-Palm Scale, Phoenicococcus marlatti, A (paper) 659-668
Biology and Economic Importance of Anastatus semiflavidus, a Recently Described Egg Parasite of Hemileuca oliviae (paper) 373-384
Bishopp, F. C., and Laake, E. W. (paper): Dispersion of Flies by Flight..... 729-766
Bishopp, F. C. (paper): Solenopotes capillatus, a Sucking Louse of Cattle Not Heretofore Known in the United States..... 797-801

Page

Blastomyces, odor on beef..... 695
Black blowfly. See *Phormia regina*.
"Black scab" of tomato. See *Bacterium exitiosum*, n. sp.
Bluegrass. See *Poa pratensis*.
Blight, Septoria, treatment of celery seed for control..... 269-372
Blowfly, black. See *Phormia regina*.
Borden, Arthur D. (paper): A Biological Study of the Red Date-Palm Scale, Phoenicococcus marlatti..... 659-668
Border effect..... 489-495
Botrytis—
cinerea—
cause of potato rot..... 211-226
enzym production..... 612
glucose as a source of carbon..... 189-210
sp., isolated from potatoes..... 828
Breeding, line, effect on variations in cotton..... 235-237
Bromus inermis, rate of culm formation.... 803-816
Bryan, Mary K. (paper): A Bacterial Budrot of Cannas..... 143-152
Bryophyllum calycinum, effect of crowngall inoculations..... 593-598
Budrot of cannas. See *Bacterium cannae*.
Bulgaricus organisms in silage..... 770
Bunyea, Hubert (paper): A Souring of Beef Caused by Bacillus megatherium..... 689-698
Caffrey, D. J. (paper): Biology and Economic Importance of Anastatus semiflavidus, a Recently Described Egg Parasite of Hemileuca oliviae..... 373-384
Calcium—
carbonate in ration for pigs..... 280-341
citrate crystals in condensed milk..... 791
phosphate—
crystals in condensed milk..... 791
in ration for pigs..... 280
sulphate, effect on alkali soil..... 271
Calcium-sodium ratio of irrigation water... 274-277
Canada field pea silage..... 771-775
Cane sugar, in sweet potato, effect of *Rhizopus tritici*..... 627-635
"Canker" of tomato. See *Bacterium exitiosum*, n. sp.
Canna indica, host of *Bacterium cannae*.... 143-152
Capsicum annuum, host of *Bacterium exitiosum*..... 123-156
Carbohydrates—
in sweet potatoes, effect of *Rhizopus tritici*, 627-635
used in respiration of storage-rot fungi... 211-226
Carbon—
dioxid, production by—
farm animals..... 351-362
respiration of storage-rot fungi..... 211-226
Rhizopus tritici..... 627-635
glucose as a source for sweet potato storage-rot fungi..... 189-210
tetrachlorid, effect on boiling point of chloroform..... 542-544
Carbon Tetrachlorid for the Removal of Parasitic Worms, Especially Hookworms (paper)..... 157-175
Carbonate, calcium, in ration for pigs..... 280-341

Page

Carrero, J. O., and Gile, P. L. (paper): Assimilation of Nitrogen, Phosphorus, and Potassium by Corn When Nutrient Salts Are Confined to Different Roots 545-573
Casein, milk, in ration for pigs 281-341
Cash, Lillian C., and Rand, Frederick V. (paper): Stewart's Disease of Corn 263-264
Castor bean. See *Ricinus communis*.
Catalese, Hydrogen-Ion Concentration, and Growth in the Potato Wart Disease (paper) 589-592
Cattle, sucking louse 797-801
Celery—
leafspot disease 185-188
seed, treatment for control of Septoria blight 369-372
See *Apium graveolens*.
Cephalothecium sp., isolated from potatoes 828
Chaetomium spp., isolated from potatoes 828
Chemical studies of silage 767-789
Chenopodium—
effect on efficacy of carbon tetrachlorid as an althelminite 167
efficacy as an anthelmintic 169-170
Chlorid—
potassium, effect on growth of storage-rot fungi 190
sodium—
effect of leaching soils 268-271
in ration for pigs 280-341
Chloris gayana, indeterminate stolon 178
Chloroform—
effect of carbon tetrachlorid on boiling point 542-544
efficacy as an althelmintic 168-170
Chlorosis of Conifers Corrected by Spraying with Ferrous Sulphate, A (paper) 153-171
Chrysomya macellaria, dispersion by flight 733-766
Chrysophlyctis endobiotica, cause of potato wart disease 589-592
Citrate—
calcium, crystals in condensed milk 791
ferric, in ration for pigs 280-341
sodium, in ration for pigs 280-341
Citric acid. See Acid, citric.
Citromyces glaber, production of citric acid 223
Citrus—
aurantium, effect of temperature on susceptibility to *Cladosporium citri* 243-253
grandis, susceptibility to *Cladosporium citri* 244
limonia, susceptibility to *Cladosporium citri* 244
nobilis var. *unshiu*, susceptibility to *Cladosporium citri* 244
sinensis, susceptibility to *Cladosporium citri* 244
Citrus scab, temperature relations 243-253
Cladosporium—
citri, temperature relations 243-253
herbarum, difference from *C. citri* 244
sp., isolated from potatoes 828
Climate, relation to potato leafroll 75-76
Collar-Rot of Tomato (paper) 179-184

Page

Colletotrichum—
lindemuthianum, effect on host tissue 612
solanicolum, isolated from potatoes 828-848
Colon-aerogenes organisms in silage 770
Coniophora cerebella, effect of hydrogen-ion concentration on growth 203
Constant-Temperature Bath for Heating Blood Serum, A 541-544
Copidosoma sp., parasite of *Recurvaria milleri* 138
Copper sulphate, effect on mold infestation of wheat 106-119
Cork formation in sweet potato 637-647
Corn—
assimilation of nutrient salts 545-573
germ in ration for pigs 281-341
silage 775-787
Stewart's disease 263-264
See *Zea mays* and *Zea mays indentata*.
Correlation and Growth in the Branches of Young Pear Trees (paper) 849-876
Corsican pine. See *Pinus laricio corsicana*.
Corticium vagum—
isolated from potatoes 828-848
temperature relations 459-482
Cotton Rootrot in the San Antonio Rotations (paper) 117-125
Cotton—
host of *Bacterium solanacearum* 262
variations 227-242
Cows, body temperature 1-28
Crab grass. See *Syntherisma sanguinalis*.
Creatinin in urine, effect of cucurbita seeds 524-528
Crowngall. See *Bacterium tumefaciens*.
Curcurbita—
maxima seeds, effects on animal metabolism 523-539
moschata seeds, effects on animal metabolism 523-539
pepo seeds, effects on animal metabolism 523-539
Cucurbita seeds, effects on animal metabolism 523-539
Culm formation in *Bromus inermis* 803-816
Cunningham, C. C. (paper): Study of the Relation of the Length of Kernel to the Yield of Corn (Zea mays indentata) 427-438
Cynodon dactylon, indeterminate stolon 178
Cyphomandra betacea, host of *Septoria lycopersici* 504
Date palm. See *Phoenix dactylifera*.
Date-palm scale. See *Phoenicococcus marlatti*.
Datura stramonium, host of *Bacterium solanacearum* 259
Day, effect of length on seedlings of alfalfa 599-608
Dendroctonus monticolae, parasitic on mountain pine 137
Determinate rhizome in timothy 177
Determinate stolon in timothy 177
Dioxid, carbon, production by—
farm animals 551-562
Rhizopus tritici 627-635
Diplodia tubericola—
cause of potato rot 211-226
glucose as a source of carbon 189-210

Page

Dipylidium sp., efficacy of carbon tetrachlorid against 164–175
Dispersion of Flies by Flight (paper) 729–766
Distinguishing Characters of the Larval Stages of the Ox-Warbles Hypoderma bovis and Hypoderma lineatum, with Description of a New Larval Stage (paper) 439–457
Ditropinotus—
aureoviridis, parasite of *Harmolita tritici* .. 405–426
flavicoxus. Syn. *Ditropinotus aureoviridis*.
Douglas fir. See *Pseudotsuga taxifolia*.
Effect of Ammonium Sulphate upon Plants in Nutrient Solutions Supplied with Ferric Phosphate and Ferrous Sulphate as Sources of Iron (paper) 701–728
Effect of Crowngall Inoculations on Bryophyllum (paper) 593–598
Effect of the Length of Day on Seedlings of Alfalfa Varieties and the Possibility of Utilizing This as a Practical Means of Identification (paper) 599–608
Effect of Ration on the Development of Pigs (paper) 279–341
Effects of Some Cucurbita Seeds on Animal Metabolism (paper) 523–539
Effect of Time of Irrigation on Kernal Development of Barley (paper) 29–45
Elachertus sp., parasite of *Recurvaria milleri*. 138
Enzym secreted by *Rhizopus tritici* 609–625
Enzyms, activity in silage 787
Eosinophiles, relation to parasitic infestation 677–688
Epiurus sp., parasite of *Recurvaria milleri* 138
Equine anemia, blood counts 684–686
Errata VI
Erythrocytes in blood of horses 678–688
Eupelmus allynii, parasite of *Harmolita tritici* 405–426
Eurytoma sp., parasite of *Harmolita tritici* 415
Euteles n. sp., parasite of *Recurvaria milleri* .. 138
Evans, Morgan W., and Oakley, R. A. (paper): Rooting Stems in Timothy 173–178
Fat—
in cucurbita seeds 526
stored on different rations 327–334
Fawcett, H. S. (paper): Some Relations of Temperature to Growth and Infection in the Citrus Scab Fungus Cladosporium citri 343–353
Ferric—
citrate in ration of pigs 280–341
phosphate, source of iron for plants 701–728
sulphate, effect on growth of storage-rot fungi 190
Ferrous sulphate—
effect on chlorosis of conifers 153–172
source of iron for plants 701–728
Fiber and seed characters of Pima cotton .. 231–233
Fiber in cucurbita seeds 526
Fir, Douglas. See *Pseudotsuga taxifolia*.
Flies—
dispersion by flight 729–766
house. See *Musca domestica*.
screw-worm. See *Chrysomya macellaria*.
stable. See *Stomoxys calcitrans*.

Page

Folsom, Donald, and Schultz, E. S. (paper): Leafroll, Net-Necrosis, and Spindling-Sprout of the Irish Potato 47–80
Fomes roseus, effect of hydrogen-ion concentration on growth 203
Formaldehyde, effect on mold infestation of wheat 106–119
Fromme, F. D., and Wingard, S. A. (paper): Varietal Susceptibility of Beans to Rust. 385–404
"Fruit scab" of tomato. See *Bacterium exitiosum*, n. sp.
Fungicides, injury to seeds with broken coats 99–121
Fungi, storage-rot—
glucose as a source of carbon 189–210
respiration 211–226
Fungus Disease Suppressing Expression of Awns in a Wheat-Spelt Hybrid, A (paper) 699–700
Further Experiments in Field Technic in Plot Tests (paper) 483–500
Fusarium—
acuminatum—
cause of potato rot 211–226
glucose as a source of carbon 189–210
coeruleum, isolated from potatoes 822–848
culmorum, isolated from potatoes 822–848
discolor var. *sulphureum*, isolated from potatoes 822–848
oxysporum, isolated from potatoes 821–848
radicicola, isolated from potatoes 821–848
solani, isolated from potatoes 822–848
trichothecioides, isolated from potatoes 827–848
Gardner, Max W., and Kendrick, James B. (paper): Bacterial Spot of Tomato 125–156
Gastrophilus spp., relation to Eosinophiles. 679–688
Germination of celery seed treated to control Septoria blight 371
Gile, P. L., and Carrero, J. O. (paper): Assimilation of Nitrogen, Phosphorus, and Potassium by Corn When Nutrient Salts Are Confined to Different Roots 545–573
Glucose as a Source of Carbon for Certain Sweet Potato Storage-Rot Fungi (paper). 189–210
Glucose—
in sweet potatoes, effect of Rhizopus tritici 633–634
source of carbon for storage-rot fungi 211–226
Godfrey, G. H., and Smith, Erwin F. (paper): Bacterial Wilt of Castor Bean (Ricinus communis L.) 255–262
Gossypium hirsutum, variations 227–249
Grass—
Bermuda. See *Cynodon dactylon*.
crab. See *Syntherisma sanguinalis*.
quack. See *Agropyron repens*.
Rhodes. See *Chloris gayana*.
Grass bacillus of Moeller, failure to produce odor on beef 695
Growth and Sap Concentration (paper) 81–98
Growth—
branches of young pear trees 849–876
effect of chlorosis 164–169
Gypsum, effect on alkali soil 271
Habrocytus n. sp., parasite of *Recurvaria milleri* 138

Page

Hahn, Glenn G., et al. (paper): A Chlorosis of Conifers Corrected by Spraying with Ferrous Sulphate 153-171
Hall, Maurice C. (paper): Carbon Tetrachlorid for the Removal of Parasitic Worms, Especially Hookworms 157-175
Hardness, relation to protein content of wheat 507-522
Harlan, Harry V., and Anthony, Stephen (paper): Effect of Time of Irrigation on Kernel Development of Barley 29-45
Harmolita—
atlantica, host of *Ditropinotus aureoviridis* .. 409
elymicola, host of *Ditropinotus aureoviridis* .. 409
grandis, host of *Ditropinotus aureoviridis* 409
secalis, host of *Ditropinotus aureoviridis* 409
tritici—
host of *Homoporus chalcidiphagus* 415-420
parasites 405-426
vaginicola, host of *Ditropinotus aureoviridis* . 409
Harter, L. L., and Weimer, J. L. (paper):
Glucose as a Source of Carbon for Certain Sweet Potato Storage-Rot Fungi 189-210
Respiration and Carbohydrate Changes Produced in Sweet Potatoes by Rhizopus tritici 627-635
Respiration of Sweet Potato Storage-Rot Fungi When Grown on a Nutrient Solution 211-226
Studies in the Physiology of Parasitism with Special Reference to the Secretion of Pectinase by Rhizopus tritici 609-625
Wound-Cork Formation in the Sweet Potato 637-647
Hartley, Carl, et al. (paper): A Chlorosis of Conifers Corrected by Spraying with Ferrous Sulphate 153-171
Harvey, R. B., and Weiss, Freeman (paper): Catalase, Hydrogem-Ion Concentration, and Growth in the Potato Wart Disease .. 589-592
Headley, Frank B., and Scofield, Carl S. (paper): Quality of Irrigation Water in Relation to Land Reclamation 265-278
Heart, effect of ration on development 297-309
Heat production of farm animals 351-362
Helianthus annuus, host of *Bacterium solanacearum* 260
Helminthosporium sp., isolated from potatoes. 828
Hemileuca—
nevadensis, host of *Anastatus semiflavidus*. 383-384
oliviae, host of *Anastatus semiflavidus* 373-384
Hemoglobin in blood of horses 678-688
Henley, R. R. (paper): A Constant-Temperature Bath for Heating Blood Serum 541-544
Heritable Variations in an Apparently Uniform Variety of Cotton (paper) 227-242
Homoporus chalcidiphagus—
host of *Ditropinotus aureoviridis* 409
parasite of *Harmolita tritici* 405-426
Hookworms, efficacy of carbon tetrachlorid against 157-175
Hordeum—
spp.—
effect of time of irrigation on development of kernels 29-45

Page

Hordeum—Continued.
spp.—continued.
relation of seed-coat injury and viability to susceptibility to molds and fungicides 99-122
vulgare, semipermeable membranes 108
Horse nettle. See *Solanum carolinense*.
Horses, blood counts 678-688
House fly. See *Musca domestica*.
Humidity—
effect on development of *Cladosporium citri* 250-252
relation to growth of Penicillium and Aspergillus 105
Hunter, Charles A. (paper): Bacteriological and Chemical Studies of Different Kinds of Silage 767-789
Hurd, Annie May (paper): Seed-Coat Injury and Viability of Seeds of Wheat and Barley as Factors in Susceptibility to Molds and Fungicides 99-122
Hybrid, wheat-spelt, suppression of awns by fungus 699-700
Hydrate, lactose, crystals in condensed milk 793-794
Hydrates, ammonium, in urine, effect of cucurbita seeds 524-528
Hydrogen-ion concentration—
in potato wart disease 589-592
of medium, effect on growth of storage-rot fungi 201-204
of solutions, effect of growing plants 707-725
Hypoderma—
bovis, larval stages 439-457
lineatum, larval stages 439-457
Hydrolaea dentipes, dispersion by flight 758-766
Ice cream, sandy crystals 791-796
Impatiens balsamina, host of *Bacterium solanacearum* 261
Indeterminate—
rhizome in timothy 177
stolon in timothy 178
Irish potato. See *Solanum tuberosum*.
Iron, relation to effect of ammonium sulphate on plants 701-728
Iron-sulphate, effect on pine seedlings 158
Irrigation, effect of time on development of barley kernels 29-45
Irrigation water, quality 265-278
Jagger, Ivan C. (paper): Bacterial Leafspot Disease of Celery 185-188
Jeffrey pine. See *Pinus jeffreyi*.
Jimson weeds. See *Datura stramonium*.
Jointworm. See *Harmolita tritici*.
Jones, Linus H., and Shive, John W. (paper): Effect of Ammonium Sulphate upon Plants in Nutrient Solutions Supplied with Ferric Phosphate and Ferrous Sulphate as Sources of Iron 701-728
Juglans—
nigra, concentration of cell sap 83-85
regia, concentration of cell sap 83-85
spp., concentration of cell sap 83-85
Kearney, Thomas H. (paper): Heritable Variations in an Apparently Uniform Variety of Cotton 227-242

Page

Kendrick, James B., and Gardner, Max W. (paper): Bacterial Spot of Tomato..... 123–156
Kernel—
barley, effect of time of irrigation on development..... 29–45
corn, relation of length to yield..... 427–438
Kidneys, effect of ration on development.. 297–309
Korstian, Clarence F., Hartley, Carl, Watts, Lyle F., and Hahn, Glenn G. (paper): A Chlorisis of Conifers Corrected by Spraying with Ferrous Sulphate..... 153–171
Kriss, Max, and Armsby, Henry Prentiss (paper): Some Fundamentals of Stable Ventilation..... 343–368
Kriss, Max (paper): Observations on the Body Temperature of Dry Cows..... 1–28
Krout, Webster S. (paper): Treatment of Celery Seed for the Control of Septoria Blight..... 369–372
Laake, E. W. (paper): Distinguishing Characters of the Larval Stages of the Ox-Warbles Hypoderma lineatum, with Description of a New Larval Stage..... 439–457
Laake, E. W., and Bishopp, F. C. (paper): Dispersion of Flies by Flight..... 729–766
Lactose—
crystals in condensed milk..... 791
hydrate crystals in ice cream..... 793–794
Laemophloeus (Cryptolesies) truncatus, enemy of *Phoenicococcus marlatti*..... 665
Larval stages of *Hypoderma* spp..... 439–457
Leafroll, Net-Necrosis, and Spindling-Sprout of the Irish Potato (paper)..... 47–80
Leafspot—
of celery..... 185–188
of tomato. See *Septoria lycopersici.*
Lemon. See *Citrus limonia.*
Lenzites sepiaria—
effect of hydrogen-ion concentration on growth..... 203
pectinase production..... 612
Leucocytes in blood of horses..... 678–688
Life History of Recurvaria milleri, the Lodgepole Pine Needle-Miner, in the Yosemite National Park, California (paper)..... 127–142
Life-History Studies of Three Jointworm Parasites (paper)..... 405–426
Linognathus vituli. Syn. *Solenopotes capillatus.*
Liver, effect of ration on development..... 297–309
Lodgepole needle-miner. See *Recurvaria milleri.*
Lodgepole pine. See *Pinus murrayana.*
Louse, sucking. See *Solenopotes capillatus.*
Lucilia sericata, dispersion by flight..... 736–766
Lungs, effect of ration on development..... 297–309
Lycopersicum esculentum, host of *Bacterium exiliosum*..... 123–156
Lymphocytes in blood of horses..... 678–688
McKay, M. B. (paper): Transmission of Some Wilt Diseases in Seed Potatoes..... 821–848
Macrosiphum solanifolii, transmission of potato leafroll..... 53, 57–59
Macrosporium solani, cause of collar-rot of tomato..... 179–184

Page

Magnesium—
in irrigation water..... 275–277
sulphate, effect on growth of storage-rot fungi..... 190
Malacosoma fraqilis, eggs host of *Anastatus semiflavidus*..... 384
Manure, effect on cotton rootrot..... 123–124
Mast cells in blood of horses..... 678–688
Masurovsky, Benjamin (paper): Effects of Some Cucurbita Seeds on Animal Metabolism..... 523–539
Medicago—
falcata, effect of length of day on seedlings. 599–608
sativa, effect of length of day on seedlings. 603–608
Mercuric-chlorid solution, reduction in strength..... 575–587
Merulius lachrymans, effect of hydrogen-ion concentration on growth..... 203
Milk—
albumin in ration for pigs..... 281–341
casein in ration for pigs..... 281–341
protein in ration for pigs..... 281–341
Moeller's grass bacillus, failure to produce odor on beef..... 695
Moisture—
effect on *Corticium vagum*..... 463–464
in silage..... 771
Molds, susceptibility of injured seeds..... 99–122
Mononuclears in blood of horses..... 678–688
Morrison, Harold (paper): Red Date-Palm Scale, Phoenicococcus marlatti: A Technical Description..... 669–676
Mosaic, relation to potato leafroll..... 74–75
Mountain-pine beetle. See *Dendroctonus monticolae.*
Mucor—
javanicus, inversion of cane sugar..... 189
racemosus—
cause of potato rot..... 211–226
glucose as a source of carbon..... 189–210
sp., isolated from potatoes..... 828
stolonifer—
effect on plant tissues..... 611
prevention of infection by wound-cork formation..... 646
Musca domestica, dispersion by flight..... 729–766
Muscina stabulans, dispersion by flight..... 729–766
Myzus persicae, transmission of leafroll..... 55–57
Naemosphaera sp., isolated from potatoes... 828–848
Nail test for sweetcorn..... 817–820
Nasturtium. See *Tropaeolum majus.*
Needle-miner, lodgepole. See *Recurvaria milleri.*
Net-necrosis of *Solanum tuberosum*..... 47–80
Nettle, horse. See *Solanum carolinense.*
Nitrate, ammonium, effect on growth of storage-rot fungi..... 190
Nitrogen—
albuminoid, in silage..... 771
amino, in silage..... 771
ammonia, in silage..... 771
assimilation by corn..... 545–573
in barley kernels, effect of time of irrigation. 31–45
in urine, effect of cucurbita seeds..... 524–528

Page

Oakley, R. A., and Evans, Morgan W. (paper): Rooting Stems in Timothy 173-178
Oakley, R. A., and Westover, H. L. (paper): Effect of the Length of Day on Seedlings of Alfalfa Varieties and the Possibility of Utilizing This as a Practical Means of Identification 599-608
Oat silage 771-775
Observations on the Body Temperature of Dry Cows (paper) 1-28
Ophyra—
aenescens, dispersion by flight 743-766
leucostoma, disperson by flight 743-766
spp., dispersion by flight 736-766
Orange—
satsuma. See *Citrus nobilis* var. *unshiu*.
shoots, coucentration of cell sap 93-94
sweet. See *Citrus sinensis*.
trifoliata. See *Poncirus trifoliata*.
Organic acids. See Acids, organic.
Osmotic concentrations in potato wart disease 589-592
Oxalic acid. See Acid, oxalic.
Oxidase activity in potato wart disease 589
Oxygen—
effect on wound-cork formation 639-641
requirements of *Bacillus megatherium* 695
Ox-warble. See *Hypoderma* spp.
Palm, date. See *Phoenix dactylifera*.
Paspalum dilatatum, determinate stolon 177
Pathogenicity of Corticium vagum on the Potato as Affected by Soil Temperature (paper) 459-482
Patterson, J. E. (paper): Life History of Recurvaria milleri, the Lodgepole Pine Needle-Miner, in the Yosemite National Park, California 127-142
Pea, Canada field, silage 771-775
Pear. See *Pyrus communis*.
Pectinase, secretion by *Rhizopus trilici* 609-625
Penicillium—
africanum, inversion of cane sugar 189
brevicaule, inversion of cane sugar 189
luteum, effect on plant tissue 611
oxalicum, production of organic acids 223
purpurdogenum, inversion of cane sugar 189
sp.—
cause of potato rot 211-226
glucose as a source of carbon 189-210
susceptibility of injured seeds 99-122
spp., isolated from potatoes 828-849
Pepper, relation of bacterial spot to *Bacterium exiliosum* 125-126
Periderm formation in sweet potato 637-647
Periola sp., isolated from potatoes 828
Pestalozzia sp., isolated from potatoes 828
Phaseolus vulgaris, varietal susceptibility .. 385-404
Phillips, W. J., and Poos, F. W. (paper): Life-History Studies of Three Jointworm Parasites 405
Phoeniccococcus marlatti—
control 666-667
distribution 659-660
natural enemies 665-666
stages 660-662

Page

Phoenix dactylifera, host of *Phoenicococcus marlatti* 669-676
Phoma sp., isolated from potatoes 828
Phormia regina, dispersion by flight 730-766
Phosphate—
calcium—
crystals in condensed milk 791
in ration for pigs 280-341
ferric, source of iron for plants 701-728
potassium—
effect on growth of storage-rot fungi 190
in ration for pigs 280-341
Phosphoric acid. See Acid, phosphoric.
Phosphorus, assimilation by corn 545-573
Pigs, effect of—
cucurbita seeds on metabolism 528-539
ration on development 279-341
Pima cotton, variations 227-242
Pine—
Austrian. See *Pinus austriaca*.
Corsican. See *Pinus laricio corsicana*.
Jeffrey. See *Pinus jeffreyi*.
lodgepole. See *Pinus murrayana*.
Scotch. See *Pinus sylvestris*.
tamarack. See *Pinus murrayana*.
western yellow. See *Pinus ponderosa*.
Pinus—
austriaca, growth on calcareous soil 154
contorta, chlorosis 155
halepensis, growth on calcareous soil 154
jeffreyi, chlorosis 153-171
laricio corsicana, chlorosis 153-171
murrayana, host of *Recurvaria milleri* 127-142
pinaster, poor growth on calcareous soil 154
ponderosa, chlorosis 153-171
sylvestrus, calcifuge tendencies 154
Plot tests, technic 483-500
Poa pratensis, rhizome 177
Polymorphonuclears in blood of horses 678-688
Pomelo. See *Citrus grandis*.
Poncirus trifoliata, susceptibility to *Cladosporium citri* 244
Poos, F. W., and Phillips, W. J. (paper): Life-History Studies of Three Jointworm Parasites 405-426
Populus tremuloides, chlorosis 155
Porte, W. S., and Pritchard, Fred J. (paper): Collar-Rot of Tomato 179-184
Relation of Horse Nettle (Solanum carolinense) to Leafspot of Tomato (Septoria lycopersici) 501-506
Potassium—
assimilation by corn 545-573
chlorid, effect on growth of storage-rot fungi 190
in irrigation water 275-277
phosphate—
effect on growth of storage-rot fungi 190
in ration for pigs 280-341
Potato aphis. See *Macrosiphum solanifolii*.
Potato—
Irish—
wart disease. See *Chrysophlyctis endobiotica*.
See *Solanum tuberosum*.

Potato—Continued. Page
sweet—
effect of *Rhizopus tritici* on respiration and carbohydrate changes..... 627–635
reduction in strength of mercuric-chlorid solution..... 575–587
storage-rot fungi, respiration..... 211–226
wound-cork formation..... 637–647
Pritchard, Fred J., and Porte, W. S. (paper):—
Collar-Rot of Tomato..... 179–184
Relation of Horse Nettle (Solanum carolinense) to Leafspot of Tomato (Septoria lycopersici)..... 501–506
Protein—
digesters in silage..... 770
in cucurbita seeds..... 526
in wheat, relation of hardness..... 507–522
milk, in ration for pigs..... 281–341
in different rations..... 327–334
Pruning, effect on concentration of cell sap..... 87–91
Pseudomonas—
apii, cause of leafspot of celery..... 185–188
destructans, enzym production..... 611
taxifolia, chlorosis..... 153–171
Pumpkin. See *Cucurbita pepo*.
Pyrus communis, growth of branches..... 849–876
Quack grass. See *Agropyron repens*.
Quality of Irrigation Water in Relation to Land Reclamation (paper)..... 265–278
Ramularia sp., isolated from potatoes..... 828
Rand, Frederick V., and Cash, Lillian C. (paper): Stewart's Diseases of Corn..... 263–264
Rate of Culm Formation in Bromus inermis (paper)..... 803–816
Ration, effect on development of pigs..... 279–341
Rectal temperatures of dry cows..... 4–28
Recurvaria milleri—
host..... 137
life cycle..... 129–137
natural enemies..... 138
Red Date-Palm Scale, Phoenicococcus marlatti: A Technical Description (paper).. 669–676
Red top. See *Agrostis alba*.
Reduction in the Strength of the Mercuric-Chlorid Solution Used for Disinfecting Sweet Potatoes (paper)..... 575–587
Reed, Howard S. (paper):—
Correlation and Growth in the Branches of Young Pear Trees..... 849–876
Growth and Sap Concentration..... 81–98
Relation of Hardness and Other Factors to Protein Content of Wheat (paper)..... 507–522
Relation of Horse Nettle (Solanum carolinense) to Leafspot of Tomato (Septoria lycopersici) (paper)..... 501–506
Reliability of the Nail Test for predicting the Chemical Compostion of Green Sweetcorn (paper)..... 817–820
Respiration and Carbohydrate Changes Produced in Sweet Potatoes by Rhizopus tritici (paper)..... 627–635
Respiration of Sweet Potato Storage-Rot Fungi When Grown on a Nutrient Solution (paper)..... 211–226
Rhizoctonia solani— Page
cause of collar-rot of tomato..... 179–184
Syn. *Corticium vagum*.
Rhizomes in timothy..... 173–178
Rhizopus—
nigricans—
inability to utilize cane sugar..... 189
susceptibility of injured seeds..... 99–122
tonkinensis, inversion of cane sugar..... 189
tritici—
cause of potato rot..... 211–226
glucose as a source of carbon..... 189–210
prevention of infection by wound-cork infection..... 642–646
secretion of pectinase..... 629–625
Rhodes grass. See *Chloris gayayna*.
Rice, host of *Sclerotium rolfsii* and *S. oryzae*. 649–658
Richards, B. L. (paper): Pathogenicity of Corticium vagum as Affected by Soil Temperature..... 459–482
Ricinus communis, host of *Bacterium solanacearum*..... 255–262
Roberts, Herbert F. (paper): Relation of Hardness and Other Factors to Protein Content of Wheat..... 507–522
Roguing, effect on variations in cotton..... 233–235
Rooting Stems in Timothy (paper)..... 173–178
Rootrot, cotton, in the San Antonio rotations..... 117–125
Rootstocks in timothy..... 173–178
Rust, varietal susceptibility of beans..... 385–404
Saccharomyces, odor on beef..... 695
Salts, assimilation by corn..... 545–573
Sandy Crystals in Ice Cream: Their Separation and Identification (paper)..... 791–796
Sap concentration, relation to growth..... 81–89
Sarcophaga spp., dispersion by flight..... 736–766
Satsuma orange. See *Citrus nobilis* var. *unshiu*.
Scab—
citrus, temperature relations..... 243–253
tomato. See *Bacterium exiliosum*, n. sp.
Scambus sp., parasite of *Recurvaria milleri*... 138
Schultz, E. S., and Folsom, Donald (paper): Leafroll, Net-Necrosis, and Spindling-Sprout of the Irish Potato..... 47–80
Sclerotinia—
cinerea, production of oxalic acid..... 631
libertiana, secretion of ferment..... 610
sp., isolated from potatoes..... 828
Sclerotium—
bataticola—
cause of potato rot..... 211–226
glucose as a source of carbon..... 189–210
oryzae, cause of stemrot of rice..... 655–657
rolfsii, cause of seedling-blight of rice..... 649–655
Scofield, C. S. (paper): Cotton Rootrot in the San Antonio Rotations..... 117–125
Scofield, Carl S., and Headley, Frank B. (paper): Quality of Irrigation Water in Relation to Land Reclamation..... 265–278
Scotch pine. See *Pinus sylvestris*.
Screw-worm fly. See *Chrysomya macellaria*.
Seed—
celery, treatment for control of Septoria blight..... 369–372

Seed—Continued. Page
characters in Pima cotton..... 231-233
relation between injury of coats and susceptibility to molds and fungicides..... 99-122
Seed-Coat Injury and Viability of Seeds of Wheat and Barley as Factors in Susceptibility to Molds and Fungicides (paper).. 99-122
Seedling-blight of rice. See *Sclerotium rolfsii.*
Septoria blight, treatment of celery seed for control..... 369-372
Septoria lycopersici—
difference from *Bacterium exitiosum*..... 127
relation to *Solanum carolinense*..... 501-506
Sequoia sempervirens, chlorosis..... 155
Serum, constant-temperature bath..... 541-544
Setaria equina, relation to Eosiniphiles..... 679-688
Sex of flies, relation to dispersion by flight. 761-762
Shive, John W., and Jones, Linus H. (paper): Effect of Ammonium Sulphate upon Plants in Nutrient Solutions Supplied with Ferric Phosphate and Ferrous Sulphate as Sources of Iron..... 701-728
Silage, bacteriological and chemical studies. 767-789
Smith, Erwin F., and Godfrey, G. H. (paper): Bacterial Wilt of Castor Bean (Ricinis communis L.)..... 255-262
Smith, Erwin F. (paper): Effect of Crown-gall Inoculations on Bryophyllum..... 593-598
Sodium—
chlorid—
effect of leaching soils..... 268-271
in ration for pigs..... 280-341
citrate in ration for pigs..... 280-341
sulphate, effect of leaching soils..... 268-271
tartrate in ration for pigs..... 280-341
Soil—
temperature, effect on *Corticium vagum*.. 459-482
transmission of potato leafroll..... 59-60
Solanum—
carolinense—
collar-rot..... 183
relation to *Septoria lycopersici*..... 501-506
mammosum, host of *Septoria lycopersici*.... 504
tuberosum—
host of *Bacterium exitiosum*..... 123-156
host of *Chrysophlyctis endobiotica*..... 589-592
leafroll, net-necrosis, and spindling-sprout..... 47-80
transmission of wilt diseases..... 821-848
Solenopotes capillatus, a Sucking Louse of Cattle Not Heretofore Known in the United States (paper)..... 797-801
Some Fundamentals of Stable Ventilation (paper)..... 343-368
Some Observations Regarding Eosinophiles (paper)..... 677-688
Some Relations of Temperature to Growth and Infection in the Citrus Scab Fungus Cladosporium citri (paper)..... 243 253
"Sore-shin fungus." See *Rhizoctonia solani.*
Souring of Beef Caused by Bacillus megatherium, A (paper)..... 689-698
Sour orange. See *Citrus aurantium.*
Soybean silage..... 775-787
Species, new..... 123-156, 179-184, 185-188
Spelt-wheat hybrid, suppression of awns by fungus..... 699-700
Sphaerococcus— Page
draperi. Syn. *Phoenicococcus marlatti.*
marlatti. Syn. *Phoenicococcus marlatti.*
Spharonema fimbriatum—
cause of potato rot..... 211-226
glucose as a source of carbon..... 189-210
Spinach aphis. See *Myzus persicae.*
Spindling-sprout of *Solanum tuberosum*.... 47-80
Spondylocladium atrovirens, isolated from potatoes..... 828-848
Sporotrichum sp., isolated from potatoes.. 828
Stable fly. See *Stomoxys calcitrans.*
Stable ventilation..... 343-368
Staphylococcus—
albus, isolated from sour beef..... 690, 694
citreus, failure to produce odor on beef.... 694
Starch—
in ration for pigs..... 281-341
in sweet potato, effect of *Rhizopus tritici*. 627-635
Stemphyllium sp., isolated from potatoes..... 828
Stemrot of rice. See *Sclerotium oryzae.*
Sterigmatocystis nigra, production of citric and oxalic acid..... 223
Stewart's Disease of Corn (paper)..... 263-264
Stolons in timothy..... 173-178
Stomoxys calcitrans, dispersion by flight.. 730-766
Storage-rot fungi—
glucose as a source of carbon..... 189-210
respiration..... 211-226
Streptococcus mastitis, failure to produce odor on beef..... 695
Studies in the Physiology of Parasitism with Special Reference to the Secretion of Pectinase by Rhizopus tritici (paper)..... 609-625
Study of the Relation of the Length of Kernel to the Yield of Corn (Zea mays indentata) (paper)..... 427-438
Stysanus stemonitis, isolated from potatoes... 828
Subsoiling, effect on cotton rootrot..... 122-123
Sucrose crystals in condensed milk..... 791
Sucking louse of cattle. See *Solenopotes capillatus.*
Sugars, in sweet potatoes, effect of *Rhizopus tritici*..... 627-635
Sulphate—
ammonium, effect on plants supplied with iron..... 701-728
calcium, effect on alkali soil..... 271
copper, effect on mold infestation of wheat 106-119
ferric, effect on growth of storage-rot fungi. 190
ferrous—
effect on chlorosis of conifers..... 153-171
source of iron for plants..... 701-728
iron, effect on pine seedlings..... 158
magnesium, effect on growth of storage-rot fungi..... 190
sodium, effect on leaching soils..... 268-271
Sulphuric acid. See Acid, sulphuric.
Sunlight, effect on enzyms..... 621-622
Sunflower. See *Helianthus annuus.*
Swanson, C. O. (paper): Effect of Ration on Development of Pigs..... 279-341
Sweetcorn, nail test..... 817-820
Sweet orange. See *Citrus sinensis.*
Sweet potato—
effect of *Rhizopus tritici* on respiration and carbohydrate changes..... 627-635

Page

Sweet potato—Continued.
reduction in strength of mercuric-chlorid solution ... 575-587
storage-rot fungi—
glucose as a source of carbon ... 189-210
respiration ... 211-226
wound-cork formation ... 637-647
Synthesiomyia brasiliana, dispersion by flight ... 737-766
Syntherisma sanguinalis, determinate stolon. 177
Tamarack pine. See *Pinus murrayana*.
Tartrate, sodium, in ration for pigs ... 280-341
Technic in plot tests ... 483-500
Temperature—
apparatus for heating blood serum ... 541-544
effect on—
Bacillus megatherium ... 695
Cladosporium citri ... 243-253
Corticium vagum ... 459-482
development of molds on wheat ... 108
enzyms ... 622
potato leafroll ... 71-73
wound-cork formation ... 640-642
in stables ... 343-368
of dry cows ... 1-28
Tetrachlorid, carbon—
effect on boiling point of chloroform ... 542-544
efficacy against hookworms ... 157-175
Thatcher, Lloyd E. (paper): A Fungus Disease Suppressing Expression of Awns in a Wheat-Spelt Hybrid ... 699-700
Thermal relations of *Bacillus megatherium* ... 695
Therms consumed, relation to therms stored 324-334
Thuja occidentalis, chlorosis ... 154
Thymol—
effect on efficacy of carbon tetrachlorid as an anthelmintic ... 166-167
efficacy as an anthelmintic ... 170-171
Tilletia foetans, suppressions of awns in wheat-spelt hybrid ... 699-700
Timothy, rooting stems ... 173-178
Tisdale, W. H. (paper): Two Sclerotium Diseases of Rice ... 649-658
Tomato—
bacterial spot ... 123-156
collar-rot ... 179-184
host of *Bacterium solanacearum* ... 262
leafspot. See *Septoria lycopersici*.
Transitionals in blood of horses ... 678-688
Transmission of Some Wilt Diseases in Seed Potatoes (paper) ... 821-848
Treatment of Celery Seed for the Control of Septoria Blight (paper) ... 369-372
Triloliata orange. See *Poncirus trifoliata*.
Triticum—
spelta cross with *T. vulgare*, suppression of awns by fungus ... 699-700
spp., relation of seed-coat injury and viability to susceptibility to molds and fungicides ... 99-122
vulgare cross with *T. spelta*, suppression of awns by fungus ... 699-700
Tropaeolum majus, host of *Bacterium solanacearum* ... 260
Two Sclerotium Diseases of Rice (paper) ... 649-658

Page

Uromyces appendiculatus, varietal susceptibility of beans ... 385-404
Vaginal temperatures of dry cows ... 4-28
Vanilla planifolia, host of *Bacterium solanacearum* ... 260
Variations in cotton ... 227-242
Varietal Susceptibility of Beans to Rust (paper) ... 385-404
Ventilation, stable ... 343-368
Vermicularia sp., isolated from potatoes ... 828
Verticillium—
albo-atrum, isolated from potatoes ... 821-848
cinnabarinum, isolated from potatoes ... 828
lycopersici, cause of collar-rot of tomato ... 179-184
Waldron, L. R. (paper): Rate of Culm Formation in Bromus inermis ... 803-816
Walnut. See *Juglans* spp.
Wart disease, potato. See *Chrysophlyctis endobiotica*.
Water—
effect on pine seedlings ... 158-159
in barley kernels, effect of time of irrigation. 31-45
irrigation, quality ... 265-278
Watts, Lyle F., et al. (paper): A Chlorosis of Conifers Corrected by Spraying with Ferrous Sulphate ... 153-171
Weather, effect on dispersion of flies by flight. 740
Weimer, J. L. (paper): Reduction in the Strength of the Mercuric-Chlorid Solution Used for Disinfecting Sweet Potatoes ... 575-587
Weimer, J. L., and Harter, L. L. (paper):—
Glucose as a Source of Carbon for Certain Sweet Potato Storage-Rot Fungi ... 189-210
Respiration and Carbohydrate Changes Produced in Sweet Potatoes by Rhizopus tritici ... 627-635
Respiration of Sweet Potato Storage-Rot Fungi when Grown on a Nutrient Solution ... 211-226
Studies in the Physiology of Parasitism with Special Reference to the Secretion of Pectinase by Rhizopus tritici ... 609-625
Wound-Cork Formation in the Sweet Potato ... 637-647
Weiss, Freeman, and Harvey, R. B. (paper): Catalase, Hydrogen-Ion Concentration, and Growth in the Potato Wart Disease ... 589-592
Westover, H. L., and Oakley, R. A. (paper): Effect of the Length of Day on Seedlings of Alfalfa Varieties and the Possibility of Utilizing This as a Practical Means of Identification ... 599-608
Western yellow pine. See *Pinus ponderosa*.
Wheat—
relation of hardness to protein content ... 507-522
See *Triticum* spp.
Wheat-spelt hybrid, suppression of awns by fungus ... 699-700
Whipworms, efficacy of carbon tetrachlorid against ... 163-175
Williams, Owen E., and Zoller, Harper F. (paper): Sandy Crystals in Ice Cream: Their Separation and Identification ... 791-796
Wilt diseases in seed potatoes ... 821-848

	Page
Wingard, S. A., and Fromme, F. D. (paper): Varietal Susceptibility of Beans to Rust	385–404
Worms, efficacy of carbon tetrachlorid against	157–175
Wound-Cork Formation in the Sweet Potato (paper)	637–647
Wright, Lewis H. (paper): Some Observations Regarding Eosinophiles	677–688
Yeast in silage	770
Yellow pine, western. See *Pinus ponderosa*.	
Zea mays—	
assimilation of nutrient salts	545–573
indentata, relation of length of kernel to yield	427–438
Zoller, Harper F., and Williams, Owen E. (paper): Sandy Crystals in Ice Cream: Their Separation and Identification	791–796
Zygodesmus sp., isolated from potatoes	828

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